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CONVERGENT FLORAL EVOLUTION IN SOUTH AFRICAN AND AUSTRALIAN PROTEACEAE AND ITS POSSIBLE BEARING ON POLLINATION BY NONFLYING MAMMALS

JOHN ROURKE[1] AND DELBERT WIENS[2]

ABSTRACT

Striking convergent evolution for a hidden (cryptic), ground flowering (geoflorous) habit in distantly related, low shrubby Australian and South African Proteaceae is interpreted as an adaptation for pollination by nonflying mammals. The cryptic, geoflorous habit is especially well developed in species groups of *Dryandra* in southwestern Australia and *Protea* in the Cape region of South Africa. Considerable circumstantial evidence exists in both regions for pollination by mouselike, often arboreal marsupials in *Dryandra* and true rodents in *Protea*. Evidence from inflorescence structure suggests the cryptic, geoflorous habit is derived from bird-pollinated species, possibly in response to fires common in the sclerophyllous communities where these genera grow. A number of floral characteristics and the occurrence in Australia of mouselike marsupials adapted to a nectar (and pollen?) diet suggests that a class of flowers has evolved for pollination by nonflying mammals. This postulated floral class possibly also extends to other Australian arboreal proteaceous and also myrtaceous genera, but in South Africa is probably restricted to *Protea*.

Pollination by nonflying mammals is largely ignored or given little credence in current treatments of pollination ecology (Faegri & van der Pijl, 1971; Proctor & Yeo, 1972). There is, however, good reason for this; all the available evidence relating to this phenomenon is either circumstantial, inferential, or anecdotal.

Nonetheless, field observations in Australia and South Africa and a subsequent search of the literature have led us to believe that true rodents and marsupials may, in fact, be the normal pollinators of several southern hemisphere proteaceous genera. Furthermore, various floral characteristics in these genera and the special adaptations for nectar feeding in some of the putative pollinators suggest structural coadaptations by both flowers and apparent pollinators. Although plans are underway to conduct definitive studies, no unequivocal evidence can be presented at this time for regular pollination by nonflying mammals, and

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that is not the intent of this paper. We hope, however, that our comments will help to reopen and stimulate research in this fascinating area of pollination biology pioneered by Porsch (1934, 1935, 1936a, 1936b) and subsequently neglected for 40 years. The purpose of this paper is fourfold: (1) to elucidate our observations and ideas on inferred pollination by nonflying mammals in the South African and Australian Proteaceae, (2) to point out the striking convergent evolution of flowering habits between southwestern Australian and South African Proteaceae of the Cape region, (3) to review some of the rather scattered and fragmentary literature on the subject, and (4) to evaluate the evidence for the existence of a class of flowers adapted to pollination by nonflying mammals.

References to the subject of pollination by nonflying mammals usually mention the arboreal Australian marsupials which apparently feed on nectar (e.g., the honey possum, *Tarsipes spencerae*) and to introduced rats suspected of pollinating a climbing pandan (*Freycinetia arborea* Gaudich.) in Hawaii. Faegri & van der Pijl (1971) and Proctor & Yeo (1972) furthermore state that no flowers appear to be adapted for pollination by nonflying mammals, although Faegri and van der Pijl mention the classic papers by Porsch (1934, 1935, 1936a, 1936b) in which he builds a case for floral adaptations to pollination by nonflying mammals in several Australian genera. Grant (1950) mentions, without comment, a "marsupial" pollinated flower class based on the proteaceous genus *Dryandra*.

In addition to rodents and mouselike marsupials, some primates may also be regular pollinators. For example, according to Coe & Isaac (1965) the baobab (*Adansonia digitata* L.) is pollinated in East Africa by the lesser bush baby (a lorisid primate). This characteristic African tree is generally considered to be bat pollinated. Petter (1962) mentions that several arboreal, mouselike lemurs (*Lemur*, *Varecia*, *Hapalemur*, *Microcebus*) visit flowers seeking nectar and are generally attracted by sweet liquids in captivity. More recently Sussman & Tattersall (1976, and personal communication) demonstrate that *Lemur mongoz mongoz* is apparently an important pollinator of introduced kapok (*Ceiba pentandra* Gaertn.) in Madagascar. F. L. Carpenter (personal communication) has data from Australia indicating that some species of *Banksia* are pollinated almost entirely by nonflying mammals, including an indigenous rat (*Rattus fuscipes*) and various marsupials.

It is not our intent to evaluate the entire literature here. There are, however, numerous instances of various mammals being observed on or around flowers (Porsch, 1934), but the nature of their activities are, in fact, virtually unknown. As Faegri & van der Pijl (1971) point out with respect to pollination by nonflying mammals "much research remains to be done to establish relationship between possible regular pollinators and the blossoms in which they work."

Floral Characteristics and Convergent Evolution of Proteaceae Putatively Pollinated by Nonflying Mammals

The most obvious Proteaceae are trees and large shrubs, e.g., *Grevillea* and *Banksia* in Australia, and *Protea* in South Africa. Less known, however, is the occurrence of species groups on both these continents with inflorescences at or near ground level (geoflorous) and typically obscured from external view by

overlying foliage (cryptic). The taxonomic distribution of these cryptic, geoflorous species is limited principally to two distinct sections of *Protea* [*Hypocephalae* and *Microgeantheae*, sensu Phillips (1912)] and some additional species of uncertain sectional classification in the Cape region of South Africa; in southwestern Australia, however, this flowering habit is associated with at least five genera (*Banksia, Conospermum, Dryandra, Isopogon,* and *Petrophile*) but is best developed in *Dryandra* [series *Aphragmia* and *Niveae*, sensu Bentham (1870)] and to a somewhat lesser extent in *Banksia*.

In these equivalent infrageneric groupings in *Protea* and *Dryandra* the growth habit is low, tufted, and often rhizomatous. The flowers occur in heads, usually at ground level, or occasionally up to 30 cm high, but in either case the heads are typically deeply hidden within the foliage of the dense and widely spreading branch systems. The heads are generally visible only if the branches are forcibly parted and the base of the plant carefully examined (Figs. 1–6). The flowers are surrounded by a prominent series of overlapping bracts forming a cup-shaped involucre. The bracts vary in color through various shades of brown and are often flushed with different dull reddish tints. An inflorescence contains perhaps 100–200 flowers, but the large spikes of *Banksia* bear several thousand individual flowers. Many of the species produce copious amounts of nectar and the heads often emit a distinctive, "nutty" or "yeasty" odor. In the cryptic, geoflorous Cape species of *Protea* the basal portions of the bracts and flowers, particularly the styles, are also markedly succulent. Excellent illustrations of *Protea* flowers (but not necessarily the growth habits) can be seen in Rousseau (1970) for South African proteas and in Erickson et al. (1973) for Australian genera.

Dryandra, as in most western Australian Proteaceae, develops no obvious succulence in the inflorescence or flowers. In general, the geoflorous habit, the cryptic positioning of the inflorescences, and the gross (though superficial) morphological similarities of the heads suggest strong convergent evolutionary tendencies. In fact, from a distance one would be hard pressed to distinguish between some species of *Dryandra* and *Protea* even though these genera represent the end points of evolution in two subfamilies of the Proteaceae, Grevilleoideae and Proteoideae, respectively, and occur on widely separated continents (Figs. 1–6).

Evidence for Rodent Pollination in South African Proteas

Field observations over a period of years of the cryptic, geoflorous species of *Protea* in the Cape area show that considerable rodent activity is associated with these species (Table 1), but is especially obvious in *P. subulifolia*. The specific rodent activities associated with this species are: (1) freshly chewed involucral bracts and styles during and just prior to anthesis (Fig. 7); (2) clearly demarcated networks of heavily used runways linking different plants within populations, and which often intertwine around flowering and old fruiting heads; and (3) occasional burrows at the base of the plants.

The runways and burrows are related to activities of the Cape striped field mouse (*Rhabdomys pumilio pumilio*). On various occasions and in different populations this animal (which is diurnal) was observed on runways between

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TABLE 1. The South African species of *Protea* in sections *Hypocephalae* and *Microgeantheae*. All species ground flowering or near ground flowering.

Hypocephalae	*Microgeantheae*	
P. subulifolia (Salisb. ex Knight) Rourke[a]	*P. acaulos* (L.) Reichard[a]	*P. montana* E. Mey. ex Meisn.
P. amplexicaulis R. Br.	*P. angustata* R. Br.	*P. restionifolia* (Salisb. ex Knight) Rycroft[a]
P. decurrens Phillips	*P. aspera* Phillips[a]	*P. revoluta* Buek ex Meisn.
P. humiflora Andrews[a]	*P. cordata* Thunb.	*P. scabra* R. Br.[a]
	P. foliosa Rourke	*P. scabriuscula* Phillips
	P. glaucophylla Salisb.	*P. scolpendrium* R. Br.
	P. intonsa Rourke[a]	*P. scorzonerifolia* Salisb. ex Knight
	P. laevis Thunb.	*P. sulfurea* Phillips[b]
	P. lorea R. Br.[b]	*P. vogtsiae* Rourke[a]

[a] Species in which evidence of rodent activities has been observed on flowers.
[b] Inclusion in this taxonomic section questionable.

flowering plants of *P. subulifolia*. That the Cape striped field mouse is attracted to the cryptic, geoflorous inflorescences of *P. subulifolia* was further demonstrated when it was live-trapped utilizing fresh flowering heads of this species as bait. In this instance traditional rodent baits such as peanut butter were ineffectual in capturing this animal.

The Cape striped field mouse apparently also visits the flowering heads of *Protea nana* (Berg.) Thunb., a low shrubby species with pendulous heads of uncertain pollination type and not a member of the geoflorous sections. The soft floral parts of *P. nana* were chewed in the same manner as *P. subulifolia* and a Cape striped field mouse was trapped at this plant within 24 h of the first noted rodent activity.

The fleshy involucral bracts and styles of the cryptic, geoflorous proteas show widespread evidence of being chewed. In one population of *P. subulifolia* 17 plants bearing 49 inflorescences with open flowers were observed in an area of approximately 30 m^2; 20 heads, or 40%, showed extensive evidence of chewed bracts and styles (Cape striped field mice were common in the area). The consistent occurrence of chewed bracts and styles in the cryptic, geoflorous proteas suggests that they function as food bodies; supporting this idea is the sweetness (at least to the human palate) of these structures. In the large, bird-pollinated proteas the bracts not only lack succulence but are markedly acrid, apparently containing high concentrations of tannin. In spite of their sweet, fleshy nature and apparent lack of tannin, all the bracts and mature styles of any head are rarely eaten. That the inflorescences are not completely destroyed suggests the presence of secondary compounds which might limit the amount of feeding as proposed by Freeland & Janzen (1974).

←

FIGURES 1–4.—1. General aspect of *Protea subulifolia* just beginning to flower (near Hermanus, Cape Prov., South Africa).—2. Cryptic, geoflorous inflorescences of *P. subulifolia* (same plant as above).—3. General aspect of *Dryandra tenuifolia* in full flower (Stirling Range, West Australia).—4. Cryptic, geoflorous inflorescences of *D. tenuifolia* (same plant as above).

Sweet, fleshy bracts are also associated with pollination in *Freycinetia* (Pandanaceae) where they reportedly attract introduced rats in Hawaii (Degener, 1945) and in other areas of the Pacific (B. C. Stone, personal communication). *Freycinetia insignis* Blume, an Asian bat-pollinated species, apparently utilizes only odor and fleshy bracts as attracting devices (Proctor & Yeo, 1972).

The sense of smell is well developed in rodents, and in view of the hidden nature of the inflorescences, odor must be the primary attracting mechanism regardless of the pollinator. Furthermore, at the time of flowering in *P. subulifolia* (late winter), the fleshy bracts and styles constitute one of the best sources of soft palatable vegetable matter in the local plant community. Thus flowering might correlate with the low point in the food cycle of rodents. The Cape striped field mouse is apparently fond of soft vegetable matter, sometimes becoming a nuisance in vegetable gardens (Roberts, 1951). As further evidence of this dietary habit, newly harvested shoots of another proteaceous shrub, *Leucodendron modestum* Williams, were observed along a typical runway and entrance to a Cape striped field mouse burrow. If the chewing activity in the flowering heads of the Cape species of geoflorous proteas is due to the Cape striped field mouse, or a similar-sized animal, pollen would surely accumulate about the head of the animal and should theoretically be capable of transfer to nearby plants. The fur of mammals should provide an excellent surface for pollen accumulation. This is demonstrated by the presence of pollen on the head of a nectar-feeding Australian marsupial, the sugar glider (*Petaurus breviceps*) (Breeden & Breeden, 1970: inside back cover). An interesting description of pollen accumulation on the Australian honey possum (*Tarsipes spencerae*) feeding on Proteaceae is also given by Vose (1972).

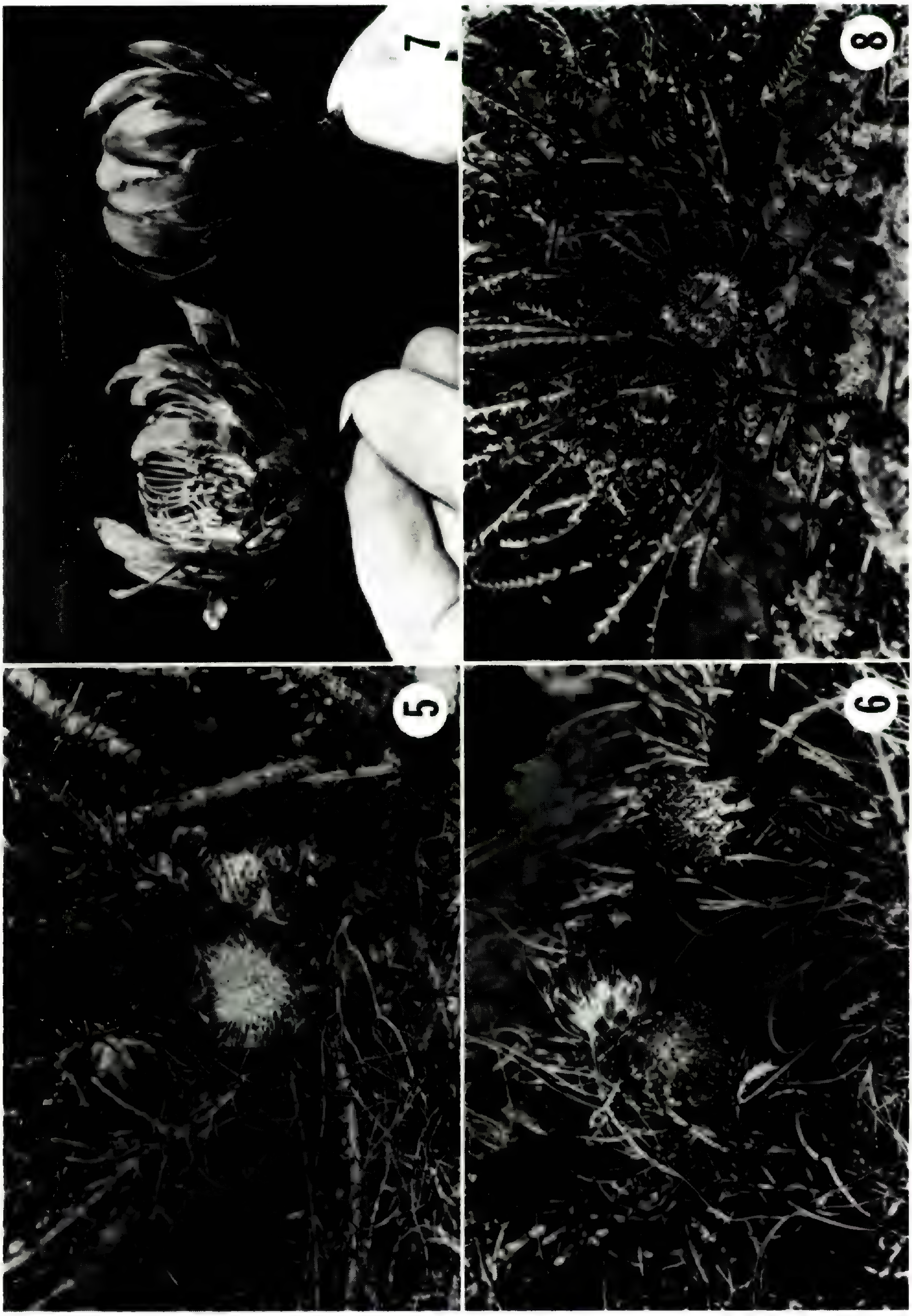
Because of its known association with *Protea* (especially *P. subulifolia*), the Cape striped field mouse is perhaps the best possibility for a mammal pollinator of the cryptic, geoflorous species of *Protea*. However, other rodents in the Cape fauna should also be examined for possible activities relating to pollination. Dr. J. Jarvis of Cape Town University (personal communication) suggests especially the following animals: *Dendromus melanotis* (climbing mouse), *Leggada minutoides* (dwarf mouse), *Otomys irroratus* (vlei otomys), and *Acomys subspinosus* (Cape spiny mouse). None of these animals, however, appear to have any special adaptations for nectar or pollen feeding.

A single case of interspecific hybridization (*P. restionifolia* × *P. humiflora*) is known among the cryptic, geoflorous species of Cape *Protea*. That such a cross occurs is proof that pollen can be transferred between these species. Furthermore, evidence of rodent activity is known in both parental species of the cross. The Proteaceae are apparently adapted for outcrossing and thus require a mechanism for pollen transfer. The family is apparently either protandrous (Rao, 1971) or self-incompatible (Horn, 1962). Pollen dispersal ultimately occurs from a specialized region of the style apex known as the pollen presenter (Rourke, 1969). This is so close to the slitlike stigmatic surface that mechanisms to prevent autogamy must be present or selfing would be the rule and pollination unnecessary.

Evidence for Marsupial and Rodent Pollination in Australian Proteaceae

Field observations of the inflorescences of *Dryandra tenuifolia* R. Br. in southwestern Australia also showed evidence of mammal activities similar to those mentioned for *Protea subulifolia* from the Cape region of South Africa; chewed heads were particularly common. The inflorescences were also odoriferous and the scent was surprisingly similar to the "yeastlike" odors prevalent in the cryptic, geoflorous species of African *Protea.* Copious nectar was not detected, but our observations were made in mid-afternoon when nectar content was possibly low. Nectar production in the Australian cryptic, geoflorous Proteaceae may be largely nocturnal to coincide with increased animal activity at that time (Morcombe, 1968). Porsch (1935) repeatedly mentions high nectar production in *Dryandra nivea* R. Br., which he observed under cultivation. He also noted nocturnal anthesis and an odor of "sour milk" or "caraway liquor" in this species. Dr. Alex George (personal communication) has also seen apparent mammal activity in the inflorescences of the cryptic, geoflorous species of *Banksia* where chewing and disturbance of the flowers appeared to be similar to our observations in South Africa. F. L. Carpenter (personal communication) also has interesting evidence that *Banksia* species in eastern Australia are largely pollinated by nonflying mammals. She correlates nonflying mammal pollination in *Banksia* with the occurrence of stiff inflexed styles (illustrated in Baglin et al., 1972) which apparently exclude foraging birds. Porsch (1935) suggested this as a feature of marsupial-pollinated banksias; he also proposed that the "basket"-like inflorescences in some dryandras were adapted to accommodate the heads of various marsupials (Fig. 8).

The situation in Australia, however, is probably more complex than in South Africa. For example, many of the large, shrubby and even arboreal Proteaceae (and also Myrtaceae) are also visited by nonflying mammals in addition to the cryptic, geoflorous species, yet the latter appear to be better adapted for pollination by nonflying mammals. Most workers probably consider these nonground flowering species to be bird pollinated (e.g., Carlquist, 1974). Admittedly many of the floral characteristics of genera such as *Banksia* do suggest bird pollination. Yet some traits clearly do not. For example, Baglin et al. (1972) state that all *Banksia* inflorescences are odoriferous, yet odor is not associated with ornithophily. Additionally, Morcombe (1968) reports that in *Banksia* nectar secretion is prolific at night, a condition hardly adapted to pollination by diurnal flower birds. Morcombe suggests that the great abundance of nocturnal insects are attracted to *Banksia* inflorescences by the copious nectar, and these in turn are what entices nonflying mammals to the flowers. Considering the highly specialized adaptations of an animal such as the honey possum (see following discussion) for a nectar (and pollen?) diet, it seems unlikely that insects would be the prime attractant, at least for this animal. However, animals such as the southwestern bush rat (a true rodent) might well be attracted by insects. But this would hardly explain why nectar secretion is abundant at night, since insects are highly unlikely pollinators of these flowers. Typically, nectar secretion is synchronized temporally for visitation by the established pollinators coadapted to that particular flower (Faegri & van der Pijl, 1971).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Derivation of Cryptic, Geoflorous Species from Ornithophilous Prototypes

Various sunbirds and the Cape sugarbird are the typical pollinators of the well-known shrubby proteas in the Cape region with large terminal inflorescences (Fig. 9). However, the cryptic, geoflorous positioning of the inflorescences in sections *Hypocephalae* and *Microgeantheae* must preclude bird pollination, since birds are attracted to flowers visually (Raven, 1972) and odor is not a characteristic of bird-pollinated flowers. In fact, sunbird or sugarbird visits to the cryptic, geoflorous proteas would violate established behavioral patterns in these birds. They are not generally known to frequent the ground, or to explore the dense interior of low shrubs which do not have exposed, colorful flowers.

Further evidence that birds are unlikely pollinators of the cryptic, geoflorous proteas is based on observations of *P. nana*. As previously mentioned, this species has pendulous, relatively small (ca. 3 cm wide), dark reddish heads. Initially one might assume that they were bird pollinated. However, a number of flowering plants of *P. nana* were observed in an area densely populated by the orange-breasted sunbird, *Nectarinia violacea* and the Cape sugarbird (*Promerops cafer*) which were feeding freely on several proteaceous shrubs with large terminal heads, and some ericas; however, no birds were observed on *P. nana*. Because the heads are pendulous, flower-visiting birds would probably have to hover to obtain nectar. Sunbirds are capable of hovering (Skead, 1967) but unlike hummingbirds, they hover clumsily. Normally they feed while clasping branches. Nonetheless, in an area with a high density of nectar-feeding birds, a great variety of flowers are normally visited in addition to the preferred species. If sunbirds and sugarbirds showed interest in the flowers of *P. nana*, at least rare visits to these plants would be expected. If nectar-seeking birds are not attracted to *P. nana*, whose inflorescences are visually conspicuous but otherwise generally resemble the cryptic, geoflorous species, it is still more difficult to believe that birds pollinate the latter group. In fact, the great majority of these South African Proteaceae with dark reddish bracts and mostly pendulous flowers might well be pollinated by nonflying mammals.

The cryptic, geoflorous proteas do retain the copious nectar supply typical of bird flowers. They differ from bird flowers, however, by (1) bearing their flowers at or near ground level in a hidden position, (2) emitting a strong "yeast-like" odor, (3) possessing much shorter flowers (ca. 1.5 cm high), and heads of smaller diameter (ca. 4–6 cm wide), and (4) the dull purplish brown coloration of the heads as opposed to the bright, vivid red and/or yellow inflorescences of the bird-pollinated species.

Essentially the same arguments apply to the situation in Australia, except

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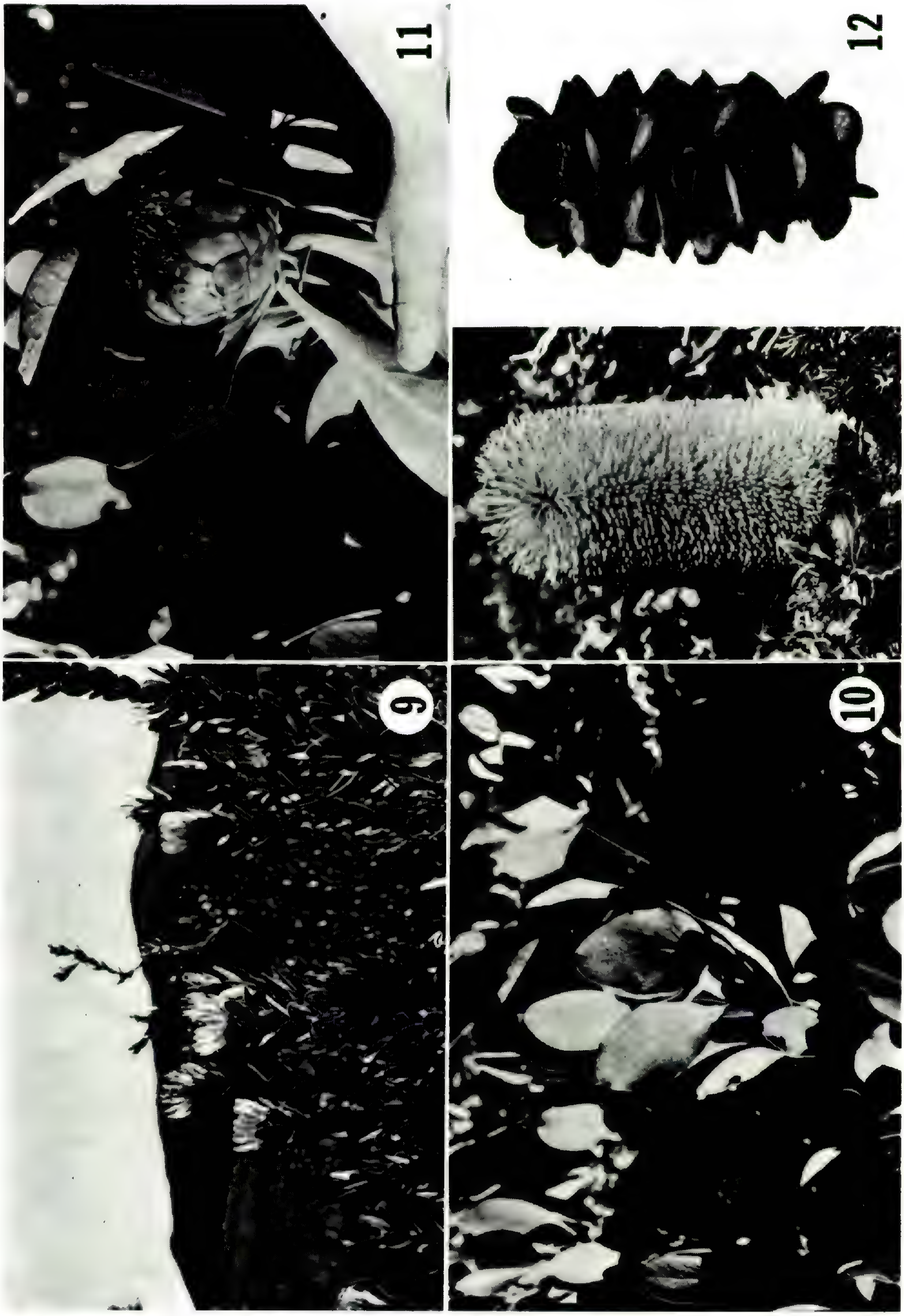
Figures 5–8.—5. Inflorescences of *Protea subulifolia* at anthesis (same plant as Figs. 1–2).—6. Inflorescences of *Dryandra tenuifolia* at anthesis (same plant as Figs. 3–4).—7. *P. subulifolia* showing chewed succulent bracts and styles (left) and intact inflorescence (right) (near Papies Vlei, Cape Prov., South Africa).—8. *Dryandra* sp., note inflexed styles forming a "basket"-shaped inflorescence (near Perth, West Australia).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that here the predominant flower birds are the honey eaters (Meliphagidae). Likewise in many of the critical genera such as *Banksia*, some species are apparently adapted for bird pollination and others for pollination by nonflying mammals.

Although we believe the cryptic, geoflorous Proteaceae are not pollinated by birds, the system nonetheless appears to have evolved from a bird-pollinated prototype. In addition to some general aspects of the inflorescence and the copious supply of nectar, the nature of the branching patterns associated with inflorescence development also supports the derived nature of the cryptic, geoflorous Proteaceae. The large, shrubby bird-pollinated proteas have terminal inflorescences, whereas the inflorescences in the geoflorous species are largely axillary. These axillary inflorescences are almost certainly derived from terminal inflorescences by progressive stem reduction. Members of the section *Pinifoliae* (which includes *P. nana*) possess intermediate forms in which the stem bearing the inflorescence is greatly shortened. Complete reduction of this stem would give rise to the almost sessile, apparent axillary inflorescences characteristic of *P. subulifolia* and other highly reduced types that occur in the geoflorous sections. Thus morphological evidence supports the proposition that the geoflorous species are derived types originating from bird-pollinated groups. Both L. A. S. Johnson and A. George (personal communications) support the notion that the cryptic, geoflorous Australian Proteaceae are also derived types.

Another interesting example of the apparently derived nature of the cryptic habit occurs in *Protea recondita* Buek ex Meisn. where floral crypsis is accomplished through an entirely different mechanism than geoflory. This species is a low shrub (up to perhaps 1 m high) with terminal inflorescences positioned similarly to the bird-pollinated proteas. The bases of the heads, however, are encircled by a cluster of unusually large, vertically oriented leaves (bracts). These bracts enfold the entire inflorescence (rather like a cabbage!) and, in effect, obscure the head from external view during anthesis (Figs. 10–11).

If the cryptic, geoflorous species of Proteaceae are adapted for pollination by nonflying mammals and were derived from bird-pollinated prototypes, what selective forces might have shifted the system in this direction? The ecological community in which these plants occur provides a possible explanation. Both the Cape region and southwestern Australia are essentially sclerophyllous, fire-adapted shrub communities. In fact, the general aspect of the two communities is remarkably similar, even to the characteristic brownish cast of the vegetation. Furthermore, both regions are extraordinarily rich floristically. Only tropical rainforests are apparently richer in plant species diversity. Both floras are also

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FIGURES 9–12.—9. *Protea compacta*, a typical bird-pollinated species at anthesis (near Papies Vlei, Cape Prov., South Africa).—10. *P. recondita*, shoot with hidden terminal inflorescence at anthesis (Kirstenbosch Botanic Garden, Cape Prov., South Africa).—11. *P. recondita* shoot with terminal inflorescence exposed behind the large, vertical bracts (same plant as Fig. 10).—12. (left) *Banksia media* (from a kodachrome by Alex George, West Australia) inflorescence at anthesis, each rounded point represents one flower, total number of flowers estimated at 4,400. (right) *Banksia* inflorescence with 34 mature fruits.

TABLE 2. Australian mammals known to visit flowers to obtain nectar and/or pollen.

Animal (all marsupials, except *Rattus fuscipes*)	References
Acrobates pygmaeus (pigmy glider)	Breeden & Breeden (1972), Carlquist (1965)
Antechinus apicalis (dibbler)	Morcombe (1968)
A. flavipes (yellow-footed antechinus)	Breeden & Breeden (1972)
Burramys parvus (mountain pigmy possum)	P. Cook (personal communication)
Cercartetus concinnus (southwestern pigmy possum)	Vose (personal communication), Ride (1970)
C. nanus (eastern pigmy possum)	Baglin et al. (1972), Breeden & Breeden (1972)
Petaurus australis (fluffy or yellow-bellied glider)	Breeden & Breeden (1972)
P. breviceps (sugar glider)	Breeden & Breeden (1970, 1972), Sleumer (1955)
P. norfolcensis (squirrel glider)	Breeden & Breeden (1972)
Phascogale tapoatafa (tuan or Wambenger)	Breeden & Breeden (1972)
Rattus fuscipes (southern bush-rat)	Morcombe (1968)
Tarsipes spencerae (honey mouse)	Morcombe (1968), Glauert (1958), Vose (1971, 1972), Ride (1970).

characterized by nutritionally depauperate soils (Wild, 1968; Loveless, 1961). Insofar as the evolution of the cryptic, geoflorous habit is concerned, however, we believe the fire-adapted nature of these communities is most important.

One way plants can survive burning is to develop rhizomaty. This condition should strongly promote ground flowering. Many, but not all, of the cryptic, geoflorous Proteaceae are rhizomatous. Hence, if rhizomaty has survival value and if there were pollinator competition between bird and nonflying mammals for floral resources, fire and the concomitant development of the rhizomatous habit could have shifted the selective advantage toward nonflying mammal pollination. It is also possible, however, that nonflying mammals, as a result of their generally more aggressive behavior, may have simply out-competed birds as pollinators and hence shifted the selective balance in this way.

A FLORAL CLASS ADAPTED FOR POLLINATION BY NONFLYING MAMMALS AND EVIDENCE FOR COEVOLUTION

Although experimental data are lacking, we believe sufficient circumstantial evidence is available to identify a class of flowers in Proteaceae adapted for pollination by nonflying mammals. Furthermore, this class of flowers has evolved independently at least twice (Africa and Australia) and at least one animal, the so-called honey possum (*Tarsipes spencerae*) has probably coevolved with this floral class in Australia. Furthermore, we believe other animals, particularly some of those in Table 2, may also have coevolved with these proteaceous plants.

The fundamental characteristics we believe might distinguish this floral class include: (1) Inflorescences as the basic units of attraction; generally they are cup-shaped heads (spikes in *Banksia*). (2) Heads typically hidden deep within the foliage, often at or near ground level; if exposed (as in *Banksia*) then with (a) structural modifications, such as stiff incurved styles or (b) nocturnal

rhythms of nectar production and/or anthesis to preclude successful nectar foraging by birds. (3) Heads about 2–8 cm wide with perhaps 100–200 flowers (several thousand in *Banksia*), and strongly attached to stems. (4) Heads producing a copious nectar supply; in some proteas also possessing apparent food bodies in the form of soft, fleshy bracts and styles acting as complementary attractants. (5) Heads odoriferous; we characterize these as "nutty" or "yeasty" in *Protea*; Porsch (1935) suggests "sour milk" and "caraway liquor" for *Dryandra*. (6) Heads with reddish brown to purplish bracts, individual flowers mostly whitish. (7) Temporal spacing of anthesis in the inflorescence, thereby limiting the number of simultaneously open flowers in the head to no more than several of the outer whorls.

Most of these characteristics were discussed previously and need no further elaboration. The most obvious feature of this putative floral class is its basic resemblance to bat-pollinated flowers (cf. Faegri & van der Pijl, 1971). The primary differences are the cryptic, geoflorous habits and the compound inflorescence as the attracting unit. There are apparently also structural modifications of the styles in the Australian species to discourage bird foraging. The basic similarities to bat flowers, however, should not be surprising since the apparent pollinators are all small mammals with perhaps generally similar energetic requirements and sensory systems [Faegri & van der Pijl (1971) point out that echo location is only poorly developed in the flower-feeding bats, Megachiroptera].

One of the strongest lines of indirect evidence supporting the idea of a class of flowers pollinated by nonflying mammals in South Africa and Australia revolves about the convergent nature of the floral characteristics in these two subfamilies of Proteaceae. If one examines the pollination syndrome of any flower class, they have essentially the same general features over the entire world. Thus convergent evolution for floral structure and habit is a necessary product of any widespread pollination system.

The variations in floral habit and structure among the Proteaceae putatively pollinated by nonflying mammals therefore reflect differences in (1) modes of locomotion to the flowers (i.e., terrestrial or arboreal movements as opposed to flying) and (2) foraging behavior. The great mobility of the nonflying mammals around flowers and the highly developed chewing apparatus (particularly among generalized feeding rodents) would probably make an attracting unit consisting of a single, large flower nonadaptive because of the destructive nature of these animals. The Proteaceae have apparently compensated for the highly destructive activities of these apparent pollinators by increasing the number of reproductive units far beyond what is necessary to maintain successful reproductive levels. In the South African cryptic, geoflorous species seed set is consistently low, usually below 5%. The same is true in the corresponding Australian genera (A. George, personal communication). In *Banksia*, the number of flowers per spike probably exceeds 4,000, yet the mature fruits are so large that it would be a physical impossibility for more than perhaps 50 to develop (Fig. 12). In addition to maximizing flower production, the flowering patterns in the heads are staggered temporally so that only several outer whorls are in anthesis simultaneously. If all the flowers opened concurrently, and in view of their sweetness

at anthesis, the entire inflorescence might be more easily destroyed by attracting a large number of pollinators.

If generalist feeding, nonflying mammals are potentially so aggressive and opportunistic in exploiting food sources, one might ask why they rarely disturb the typically bird-pollinated South African proteas. First, the bird-pollinated species are not odoriferous and the terminal inflorescences are typically borne high above ground level (Fig. 9); thus most such inflorescences probably escape detection. Another aspect, however, is the presence in some species (especially section *Speciosae*) of a thick layer of trichomes over the top of the heads. Such a dense layer of trichomes might serve to discourage mammals from chewing to the base of the heads where the nectar is located and thus act as a kind of "mammal guard." Birds, of course, easily probe through this layer with their long bills. The heads are also closely surrounded by stiff leathery bracts, which also have considerable trichome development along their margins, where chewing is most apt to be initiated. Excellent illustrations of these phenomena are found in Rousseau (1970). Finally, the acrid taste of these bracts, as opposed to the sweetness of the bracts and styles in the cryptic, geoflorous species, might also be important.

Many observations of nonflying mammals on Proteaceae (and also Myrtaceae) are reported in the popular natural history literature of Australia, e.g., Serventy & Raymond (1974) and Russell (1974) (see also references in Table 2). In fact, so prevalent are these observations that many Australian biologists take this pollination system essentially for granted (Morcombe, 1968; Johnson & Briggs, 1975). To our knowledge, however, no definitive data to establish this relationship has yet been published. Of the nonflying mammals listed in Table 2 as potential pollinators, the honey possum or noolbenger (*Tarsipes spencerae*), appears to be the best known and apparently the most highly specialized for nectar (and pollen?) feeding. This amazing animal was studied in captivity by Glauert (1958) and Vose (1972, 1973), who include illustrations. Because no comprehensive review of its spectacular adaptations for nectar (and pollen?) feeding is evidently available, a brief resumé of these characteristics taken from the sources quoted above and from Carlquist (1965) might be useful.

The head and body are small (6–8 cm long and weighing only 7–11 g). The elongated, tapering snout composes two-thirds of the head. The ears are set far back on the head and the nose is grooved. These features no doubt allow the honey possum to probe deeply into flowers. The tail is longer than both the head and body (8–10 cm) and is prehensile, while the digits of the limbs are slender and elongated for grasping; both characteristics being excellent modifications for the arboreal habit. But it is in the mouth where the most fascinating adaptations for nectar (and pollen?) feeding exist.

The tongue is extensible to twice its normal length, tapered, slightly serrated on the margin and brushed at the tip (Fig. 2 in Vose, 1972). It is exserted through a funnellike structure at the tip of the tapering snout where the lips are modified into flanges. The palate is characterized by ridges which apparently remove accumulated nectar (and pollen?) from the tongue when it is retracted. The jaws are much reduced and dentition rudimentary. Only the upper canines and lower incisors are developed and these appear to function largely in orienting

the tongue during retraction. There is no caecum, such a digesting organ for solid food apparently being superfluous in an animal adapted to a nectar diet. Additional structural and especially physiological adaptations for nectar (and pollen?) feeding will no doubt be discovered when more extensive studies are conducted. The evidence that *Tarsipes* is adapted to a diet derived from flowers (and probably occasional insects) is overwhelming. As a corollary, the conclusion that *Tarsipes* has coevolved as a pollinating agent with various proteaceous (and myrtaceous) genera is inescapable.

Sleumer (1955) states that in both northeastern Australia and southeastern New Guinea, the sugar glider (*Petaurus breviceps*), along with several flower birds, are always associated with flowering *Banksia dentata* and the myrtaceous genera *Melaleuca* and *Eucalyptus*. According to Sleumer, the sugar glider sucks nectar with a "wormshaped" tongue, suggesting possible anatomical adaptations for a nectar diet.

Although reference has so far only been made to the cryptic, geoflorous proteas, other Australian proteaceous and myrtaceous genera such as *Eucalyptus* and *Melaleuca* are known, or suspected, to be visited by various nonflying mammals. For example, *Tarsipes* reportedly feeds on *Hakea* and *Beaufortia* (Morcombe, 1968). Vose (1972) also lists species of *Callistemon* and *Grevillea* from which *Tarsipes* will extract nectar in captivity. Additional reports of nectar sources for flower-visiting marsupials include *Dryandra* (Glauert, 1958) and *Angophora* (Porsch, 1934).

If the honey possum and possibly also other small arboreal marsupials have apparently coevolved in Australia, why has coevolution between Proteaceae and true rodents not occurred in South Africa? One obvious reason is that the proteas in South Africa ostensibly pollinated by nonflying mammals do not flower throughout the year. The flowering period for these plant groups is limited primarily to late winter or early spring, as previously mentioned. Thus coevolution is impossible because the flowers do not provide a constant food source for these animals which are active throughout the year. Furthermore, it is likely that plants can adapt relatively easily to a generalized feeder, such as many rodents, and that pollination can be reasonably well assured by offering high rewards and reducing competition with other food sources in the community by flowering at the low point in the food cycle.

Potential Pollination by Nonflying Mammals in Other Plant Groups

Discussion in this paper is confined essentially to the possible pollination of Proteaceae by nonflying mammals in South Africa and Australia because we observed many of these species and genera in the field. In any overall consideration of the phenomenon, however, other plant groups should not be overlooked. If pollination by small, arboreal marsupials occurs in Australian Proteaceae, it probably also occurs in Myrtaceae. The mouselike lemurs on Madagascar (Sussman & Tattersall, 1976) which take nectar from introduced kapok must be adapted for visiting similar indigenous flowers as well. Porsch (1935) mentions Madagascan *Symphonia* (Guttiferae) as a possible flower adapted for pollination by

nonflying mammals. He also discusses other families, e.g., Bombacaceae and Lecythidaceae, which also might have adaptations for pollination by various nonflying mammals. Porsch's observations merit careful reconsideration, and, especially, critical field studies to test his hypotheses.

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EVOLUTION OF SEED SIZE, SHAPE, AND SURFACE ARCHITECTURE IN THE TRIBE EPILOBIEAE (ONAGRACEAE)[1]

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Abstract

The seeds of more than half of the approximately 210 species of Onagraceae tribe Epilobieae were examined with the scanning electron microscope. The six species of *Boisduvalia* have irregularly angular-fusiform seeds with convex, flat, irregularly polygonal surface cells in two species and an irregularly striated reticulum formed by the unevenly joining walls of the surface cells in the four others. They are similar to one another and sharply distinct from those of *Epilobium*, although the relationship between the genera is undoubtedly close. The seeds of *Epilobium* fall in seven groups: (1) large, obovoid seeds with a more or less prominent micropylar constriction, in three small sections of generalized xerophytes and in one species, *E. rigidum*, of sect. *Epilobium*; (2) smaller papillose seeds in over half of the other species; (3) foveolate seeds, independently evolved in many species; (4) obovoid-patelliform seeds in four Australasian species; (5) irregularly reticulate seeds in one subsection of *Epilobium* sect. *Chamaenerion*; (6) ridged seeds in a phylogenetically coherent group of North American origin; (7) finely papillose, distinctive seeds in sect. *Crossostigma*. More or less prominent chalazal beaks have evolved in some species. From xerophytic ancestors, *Epilobium* has evolved a highly successful group of mesophytes in sect. *Epilobium* that have achieved worldwide distribution. This trend seems to have been accompanied by an increase in seed number and a concomitant decrease in seed size.

The well-marked tribe Epilobieae, one of six that make up the family Onagraceae, includes some 200 species of *Epilobium*, of worldwide distribution; and six of *Boisduvalia*, five of western North America, with one common to Argentina, and one additional species restricted to western South America. The western North American *Zauschneria*, often recognized as distinct from *Epilobium*, is based on a red-flowered, bird-pollinated species of one of the constituent groups of *Epilobium*. *Zauschneria* has accordingly been reduced to the status of a section of *Epilobium* (Raven, 1976). Of the six sections of *Epilobium*, two, with a total of three species, consist of annuals and are restricted to western North America; two others, with a total of four species, are generalized xerophytic perennials of western North America; one, *Chamaenerion*, includes seven species of Eurasia, two of which extend to North America; and the remaining one, sect. *Epilobium*, consists of some 185 species, found on every continent except Antarctica, but especially well represented at high altitudes and high latitudes.

The surface sculpturing of the seeds of *Epilobium* has long been employed as an important taxonomic character (cf. Haussknecht, 1884; Samuelsson, 1923,

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1930; Munz, 1965), and it is natural that these seeds have been investigated in recent years with the scanning electron microscope (SEM). The regional or more limited studies that have been concerned with the scanning electron microscopy of the seeds of *Epilobium* are the following: Berggren (1974), Denford & Karas (1974), Skvortsov & Rusanovitch (1973, 1974), Raven & Raven (1976), and Seavey et al. (1977). To a certain extent, these studies have provided background for the present more comprehensive effort.

In addition to the surface variations seen with the SEM, seeds of Epilobieae vary considerably in size and shape. It is the purpose of our report to evaluate these seed characters against a background of other lines of systematic investigation, including cytology, morphology, and biogeography. Included in this analysis are more than half of the approximately 210 species of Epilobieae, representing the entire range of diversity; four of the seven species of sect. *Chamaenerion*; and all species of the remaining sections of *Epilobium*, as well as all six species of *Boisduvalia*.

The seeds of all but one of the species of *Epilobium* possess a tuft of trichomes, the coma, on their chalazal (distal) end, whereas none of the species of *Boisduvalia* have a coma. Although some variation exists in the color and relative strength of attachment of the coma (cf. Raven & Raven, 1976), no differences in its ultrastructure have been detected and this feature of seed anatomy is not dealt with in the present report.

Materials and Methods

Seeds were collected from recently grown garden plants or from herbarium sheets. The coma was removed in most cases, but left intact if removal damaged the chalazal end of the seed. The seeds were then mounted on aluminum stubs with double-sticky tape, coated with gold/platinum in a Technics Hummer I and examined with a Cambridge Stereoscan Mark 2A scanning electron microscope, operated at an accelerating voltage of 20KV, at the Department of Pathology, Medical School, Washington University. About 75 other samples were photographed in the same way in the Electron Microscope Section of the Physics and Engineering Laboratory, D.S.I.R., Lower Hutt, New Zealand, and the results of examining these photographs are likewise incorporated into the present paper.

Four to six seeds of each sample were mounted and inspected. Little variation within samples was evident, and the seed photographed was in all cases judged to be typical for the sample. Photographs were taken at approximately 60×, 240×, and 1200×. The higher magnification photographs were taken near the center of the seed, but since little variation is usually evident over the surface of this seed, this practice was not strictly followed in all cases.

A list of specimens from which seeds were taken for the illustrations (Figs. 1–210) in this paper is presented in Table 1. Voucher numbers are given in the legends of Figs. 1–210 only when more than one collection is listed in Table 1. Bars at the top of each plate indicate, respectively, 0.5 mm, 125 μm, and 25 μm.

TABLE 1. Voucher information for species of *Boisduvalia* and *Epilobium* illustrated in this paper. *M* and *G* numbers refer to garden planting numbers, used also on herbarium vouchers; *R* numbers are *Raven* collections. All vouchers are deposited at the Missouri Botanical Garden (MO), unless otherwise indicated.

Boisduvalia cleistogama Curran. U.S.A., Calif., Yolo Co., *Crampton 9222.*

B. densiflora (Lindl.) S. Wats. U.S.A., Calif., Fresno Co., near Auberry, *Seavey in 1974, M130.*

B. glabella (Nutt.) Walp. U.S.A., Calif., Solano Co., near Elmira, *Crampton 9219.*

B. macrantha Heller. U.S.A., Calif., Modoc Co., near Lookout, *Seavey in 1974, M137.*

B. stricta (A. Gray) Greene. U.S.A., Calif., Fresno Co., near Auberry, *Seavey in 1974, M133.*

B. subulata (Ruiz & Pavón) Raimann. Chile, Ñuble, *Cheese & Watson 4405, M158.*

Epilobium alpestre (Jacq.) Krock. Switzerland, Canton Vaud, seed from Conservatoire et Jardin botaniques, Genève, 1972–1788, *M31.*

E. alsinifolium Vill. U.S.S.R., Transcarpathia, *Skvortsov in 1968* (DS), *R26179.*

E. amurense Hausskn. Japan, Pref. Yamanashi, Hayakawa-cho, *Deguchi in 1974, M80.*

E. anagallidifolium Lam. U.S.S.R., E. Chukotka, Iskaten Range, *Kozhevnikov in 1972, M718.*

E. angustifolium L. subsp. *circumvagum* Mosquin. U.S.A., Calif., Onion Valley, *Twisselmann 5825* (CAS).

E. atlanticum Litard. & Maire. Spain, Sierra Nevada, *R26166.*

E. behringianum Hausskn. Alaska, Kiska Quad., Buldir Is., *Dick 414, M294.*

E. billardierianum Sér. subsp. *billardierianum*. New Zealand, Nelson, *Brockie CHR199322, M4.*

E. canum (Greene) Raven subsp. *garrettii* (A. Nels.) Raven. U.S.A., Utah, Washington Co., Zion Natl. Park, *Seavey in 1974, G865.*

E. canum subsp. *canum*. U.S.A., Calif., Santa Barbara Co., Santa Cruz Is., seed from Rancho Santa Ana Botanic Garden, *G844.*

E. canum subsp. *septentrionale* (Keck) Raven. U.S.A., Calif., Humboldt Co., Trinity River, *Tracy 5974.*

E. canum subsp. *latifolium* (Keck) Raven. U.S.A., Calif., Lake Co., Snow Mt., *Seavey in 1974, G807.*

E. chilense Hausskn. Chile, Prov. Cautín, near Lake Icalma, *Zöllner 7868, M108.*

E. ciliatum Raf. U.S.A., Oregon, Josephine Co., near O'Brien, *Seavey 1119.*

E. coloratum Biehler. Seeds from Copenhagen Botanical Gardens, *M88.*

E. davuricum Fisch. Canada, Yukon Terr., *Porsild 306* (UBC); U.S.S.R., S.E. Chukchi Peninsula, *Yurtsev & Raszhivin in 1972.*

E. denticulatum Ruiz & Pavón. Peru, Pampa to Yamobamba, ca. 70 km E. of Trujillo, *Conrad 2715, M83.*

E. dodonaei Vill. U.S.S.R., no voucher.

E. duriaei Gay ex Godron. Spain, Puerto Ventana, Oviedo, *Merxmüller & Grau 21360, R26258.*

E. exaltatum Drew. U.S.A., Calif., Siskiyou Co., *Seavey in 1971, M409*; Washington, Clallam Co., *Seavey 1111, M559.*

E. fauriei H. Lév. Japan, Tottori Pref., *Yamamoto in 1970, M265.*

E. foliosum (Nutt. ex Torr. & A. Gray) Suksd. U.S.A., Oregon, Douglas Co., *Raven 19089.*

E. glaucum Phil. Chile, Prov. Curicó, Dept. Curicó, *Marticorena, Matthei & Rodríguez 1, M68.*

E. gunnianum Hausskn. Australia, N.S.W., New England Natl. Park, *Raven & Englehorn 25853.*

E. hirsutum L. U.S.S.R., E. Kazakhstan, Altai Mts., *Belianina in 1969* (DS), *M58.*

E. hirtum Samuelsson. Peru, 20 km W. of Arequipa, *Averett 1004, M341.*

E. hornemannii Reichenb. s. lat. U.S.S.R., E. Chukchi Peninsula, *Yurtsev & Sytin in 1971.*

E. komarovianum H. Lév. New Zealand, near Mt. Cook, *Raven & Engelhorn. CHR-199430* (MO).

E. latifolium L. U.S.S.R., Dist. Barguzin, *Makeeva in 1971.*

E. leiophyllum Hausskn. Afghanistan, S. of Unai Pass, *Breckle A2717, G352.*

E. luteum Pursh. Alaska, Juneau, *Shumway in 1891* (GH).

E. minutum Lindl. ex Lehm. U.S.A., Calif., Plumas Co., *Howell 51156.*

TABLE 1. (continued)

E. nesophilum Fern. Canada, St. Phillips, Newfoundland, *Olsen in 1974, M121.*
E. nevadense Munz. U.S.A., Nevada, Clark Co., Charleston Mts., *Seavey in 1974, G808.*
E. nivium T.S. Brandegee. U.S.A., Calif., Lake Co., Snow Mts., *Seavey in 1974, G866.*
E. nutans Schmidt. Czechoslovakia, W. Bohemia, *Kral in 1967, G23.*
E. obcordatum A. Gray subsp. *obcordatum.* U.S.A., Calif., Mono Co., Oneida Lake, *McMillan 59-1* (CAS).
E. obcordatum subsp. *siskiyouense* Munz. U.S.A., Calif., Siskiyou Co., Sacramento River headwaters, *Pringle 1882* (NY).
E. obscurum Schreb. England, Surrey, *Raven 26092, M2.*
E. oreganum Greene. U.S.A., Oregon, Josephine Co., near O'Brien, *Seavey 1117.*
E. oregonense Hausskn. U.S.A., Calif., Mono Co., Rock Creek, *Seavey in 1970, G350.*
E. palustre L. U.S.S.R., Chukchi Peninsula, *Yurtsev & Raszhivin in 1972.*
E. paniculatum Nutt. ex Torr. & A. Gray. U.S.A., Oregon, Josephine Co., near O'Brien, *Seavey in 1975, M554.*
E. cf. *pauciflorum* Samuelsson. Chile, on the pass of Loleo, *Zöllner 6245, M110.*
E. pictum Petrie. New Zealand, Tasman Valley, *Raven & Wilson 25617.*
E. platystigmatosum C. B. Robinson. Taiwan, Hualien Co., *K. S. Hsu 1714, G657.*
E. pylaieanum Fern. Canada, Newfoundland, St. Stephen's, *Olsen in 1974, M127.*
E. pyrricholophum Fr. & Sav. Japan, Nikko, seeds from University of Tokyo Botanical Garden, *Tochi, M73.*
E. rigidum Hausskn. U.S.A., Oregon, Josephine Co., *Seavey 1116*; Calif., Del Norte Co., *Curtis 1* (RSA).
E. scalare Fern. Canada, Newfoundland, Highlands of St. John, *Fernald & Long 28728* (GH).
E. shiroumense Matsum. & Nakai. Japan, Pref. Yamanashi, *Deguchi in 1974, M81.*
E. stereophyllum Fresen. Kenya, Aberdare Natl. Park, *Raven 26164, M78.*
E. stevenii Boiss. Iran, Azerbaijan Prov., *Termé in 1971.*
E. strictum Muhl. Canada, Ottawa, Ontario, Carleton Co., *Frankton in 1974, M65.*
E. suffruticosum Nutt. U.S.A., Wyoming, Teton Co., Teton Natl. Park, *Raven 26464.*
E. treleasianum H. Lév. British Columbia, near Bouff, *Price 1900* (GH).
E. sp. Argentina, Estancia Moat, Tierra del Fuego, *Moore 1686, M254*; like *E. cunninghamii* Hausskn. except for pubescence.

OBSERVATIONS

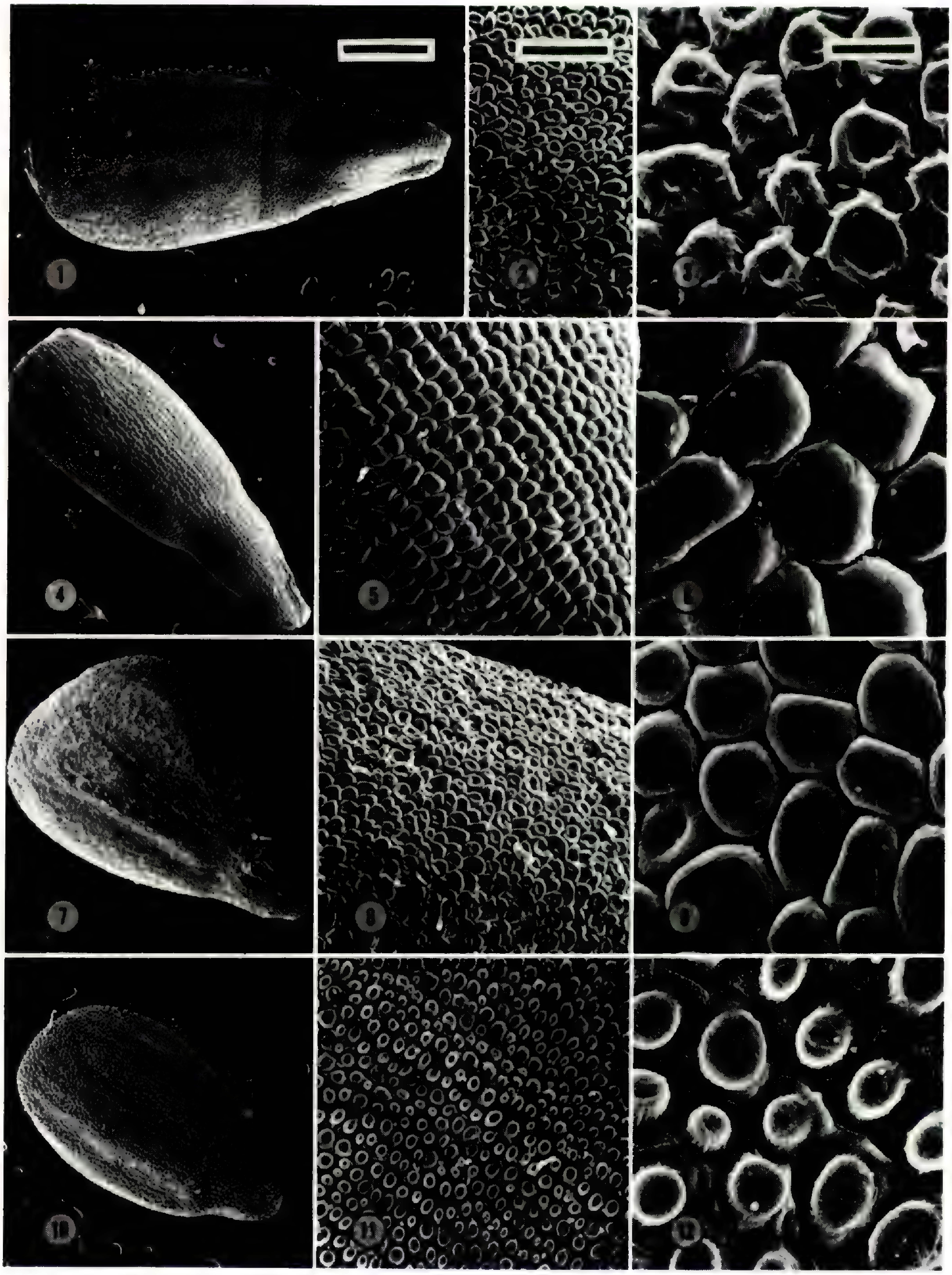
I. *Epilobium*

The results are presented according to the sections recognized by Raven (1976).

Sect. *Cordylophorum* (3 species):

Epilobium nevadense (Figs. 1–3), *E. nivium* (Figs. 7–9), and *E. suffruticosum* (Figs. 4–6), all have relatively large seeds (2.0–2.7 mm) with a prominent constriction toward the micropylar end. The seeds of *E. nevadense* are obovoid, those of *E. suffruticosum* clavate, and those of *E. nivium* broadly obovoid. The cells at the point of attachment of the coma form a distinct, although small, neck region at the chalazal end.

The surface cells of *E. nevadense* (Fig. 3) are unique in shape. The center of each cell is occupied by a thick, crater-shaped, apparently collapsed tangential wall. The surface cells of the two other species are entirely convex, giving a cobblestone appearance at high magnification (Figs. 6, 9). With respect to seed characters, *E. suffruticosum* resembles *E. nevadense* more than either resembles *E. nivium.*



FIGURES 1–12. Scanning electron micrographs of seeds of *Epilobium*, sects. *Cordylophorum* and *Xerolobium*.—1–3. *E. nevadense* (*Cordylophorum*).—4–6. *E. suffruticosum* (*Cordylophorum*).—7–9. *E. nivium* (*Cordylophorum*).—10–12. *E. paniculatum* (*Xerolobium*).

Sect. *Xerolobium* (1 species):

The large, broadly obovoid seeds of *E. paniculatum* (Figs. 10–12) also have a prominent constriction toward the micropylar end. The tangential walls of the surface cells have a centrally situated convex prominence (Fig. 12). The seeds of this species are similar to those of *E. nivium*. The neck region is inconspicuous.

Sect. *Zauschneria* (1 species):

The seeds of four of the six subspecies of *Epilobium canum* are presented in Figs. 13–24. Resembling those of the preceding section, these seeds are large and broadly obovoid; and, like all of the species of the preceding two sections, they have a constriction toward the micropylar end. The neck region is inconspicuous, but, as in those of the preceding sections, distinct, especially when viewed from a low angle (e.g., *E. canum* subsp. *canum*, Fig. 199). The tangential walls of the surface cells are entirely convex with little radial wall evident, except for subsp. *canum* (Figs. 16–18), in which the tangential walls are convex but sunken within prominent radial walls.

Sect. *Chamaenerion* (7 species):

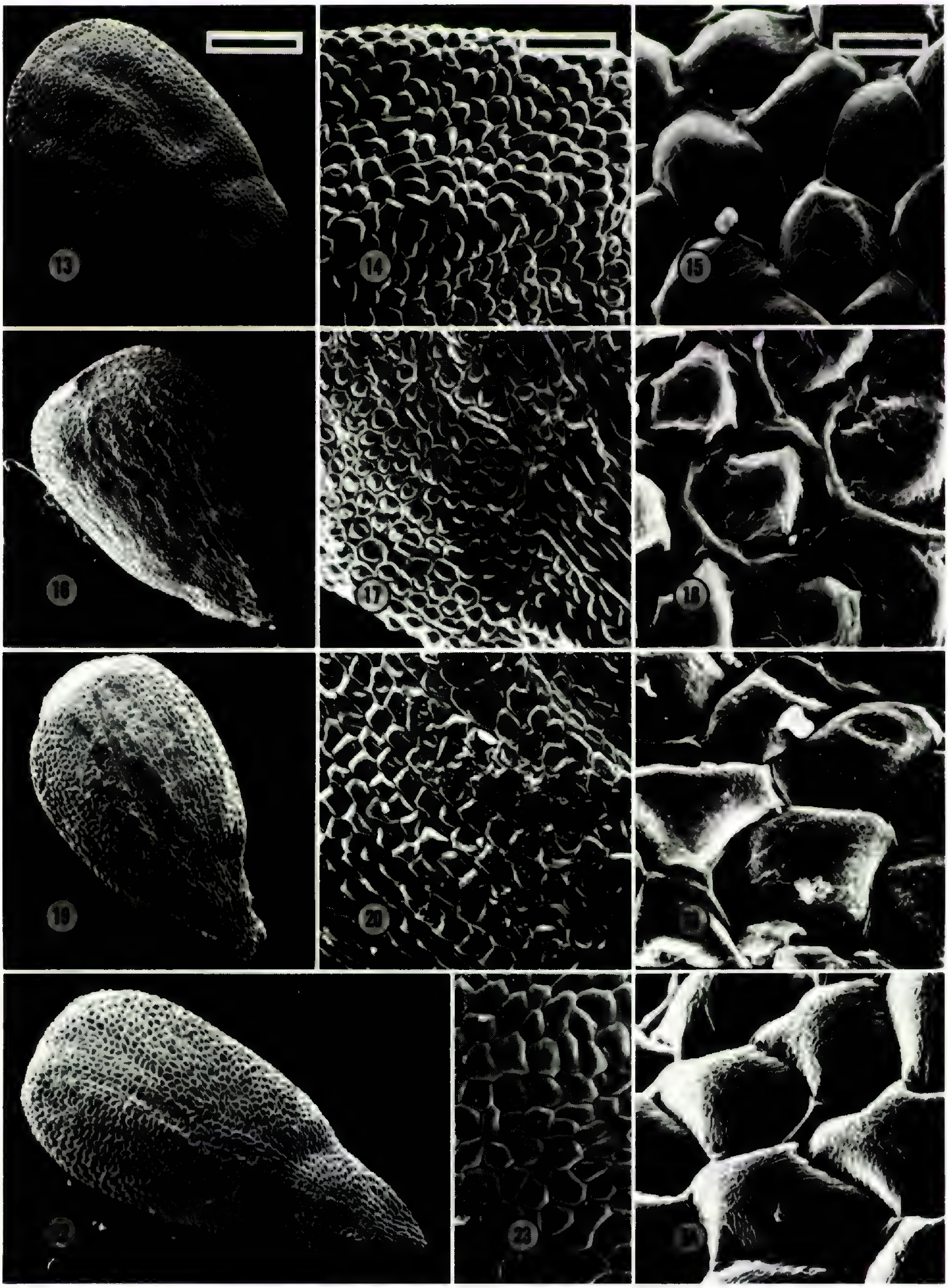
The seeds of this section are small (1.0–1.8 mm) and relatively narrower than those of the preceding three sections (Figs. 25–36). The neck region is evident in dorsal view and is composed of irregularly constricted chalazal end cells (e.g., *E. latifolium*, Fig. 209). The surface cells of the three species of subsect. *Leiostylae*, *E. angustifolium* (Figs. 25–27), *E. conspermum* Hausskn., and *E. latifolium* (Figs. 28–30), lack convex tangential walls, and the major feature of the surface is the irregularly polygonal reticulum formed by the radial walls (Figs. 27, 30). The two species of subsect. *Rosmarinifolium* we examined, *E. stevenii* (Figs. 31–33) and *E. dodonaei* (Figs. 34–36) are of approximately the same size and shape, but the surface tangential walls appear as raised, irregularly compressed areas in the center of prominent regularly polygonal radial walls.

Sect. *Crossostigma* (2 species):

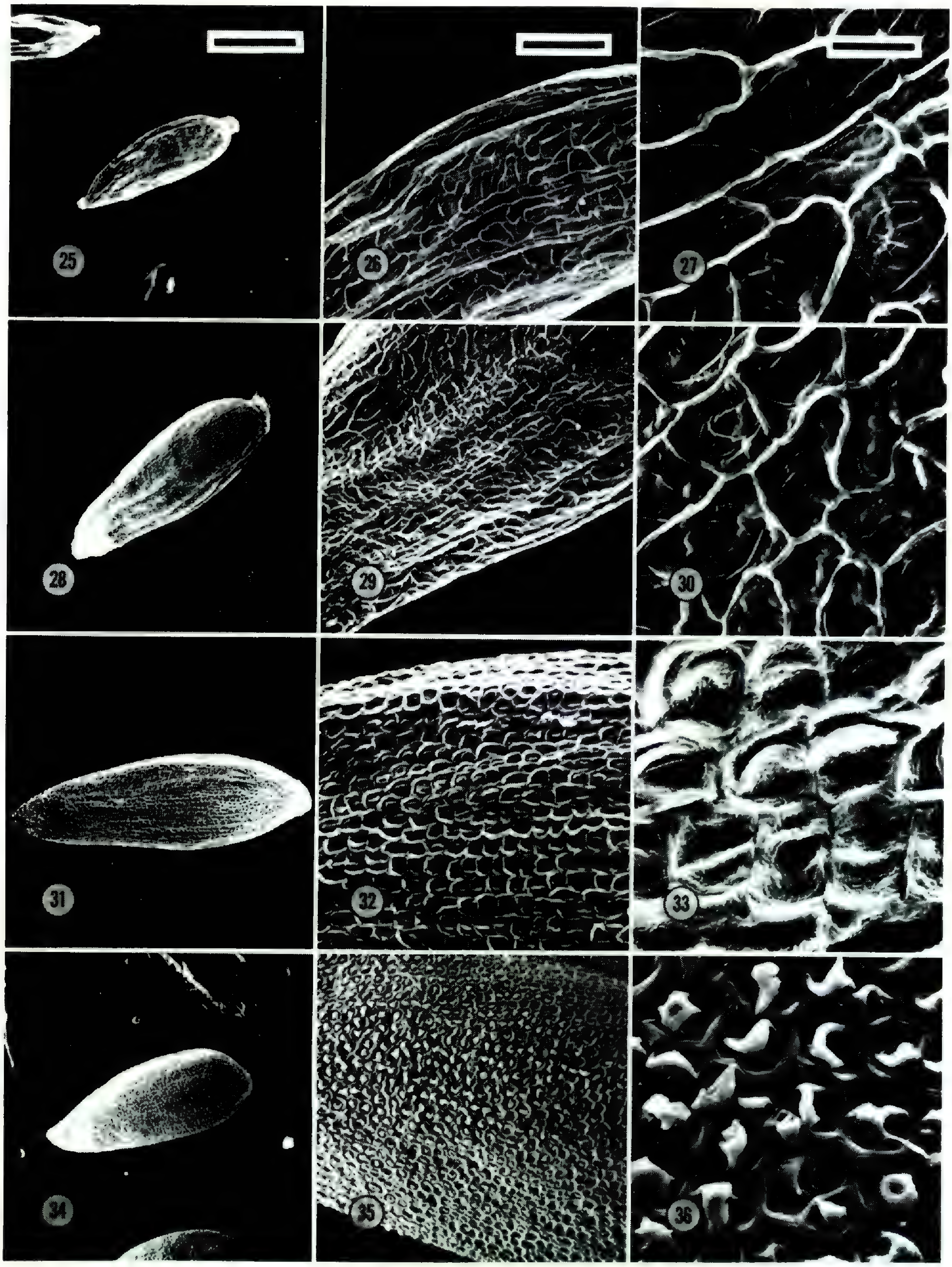
These small, obovoid seeds, blunt at both ends, are unique in the tribe in their very finely papillose surface cells (Seavey et al., 1977). The surface cells of *E. minutum* (Figs. 193–195) are concave and very finely papillose over the tangential walls as well as the prominent reticulate radial walls (Fig. 195), whereas the surface in *E. foliosum* (Figs. 196–198) has isolated convex, smooth tangential walls surrounded by finely papillose, elevated radial walls. The neck region in both species is inconspicuous.

Sect. *Epilobium* (ca. 185 species):

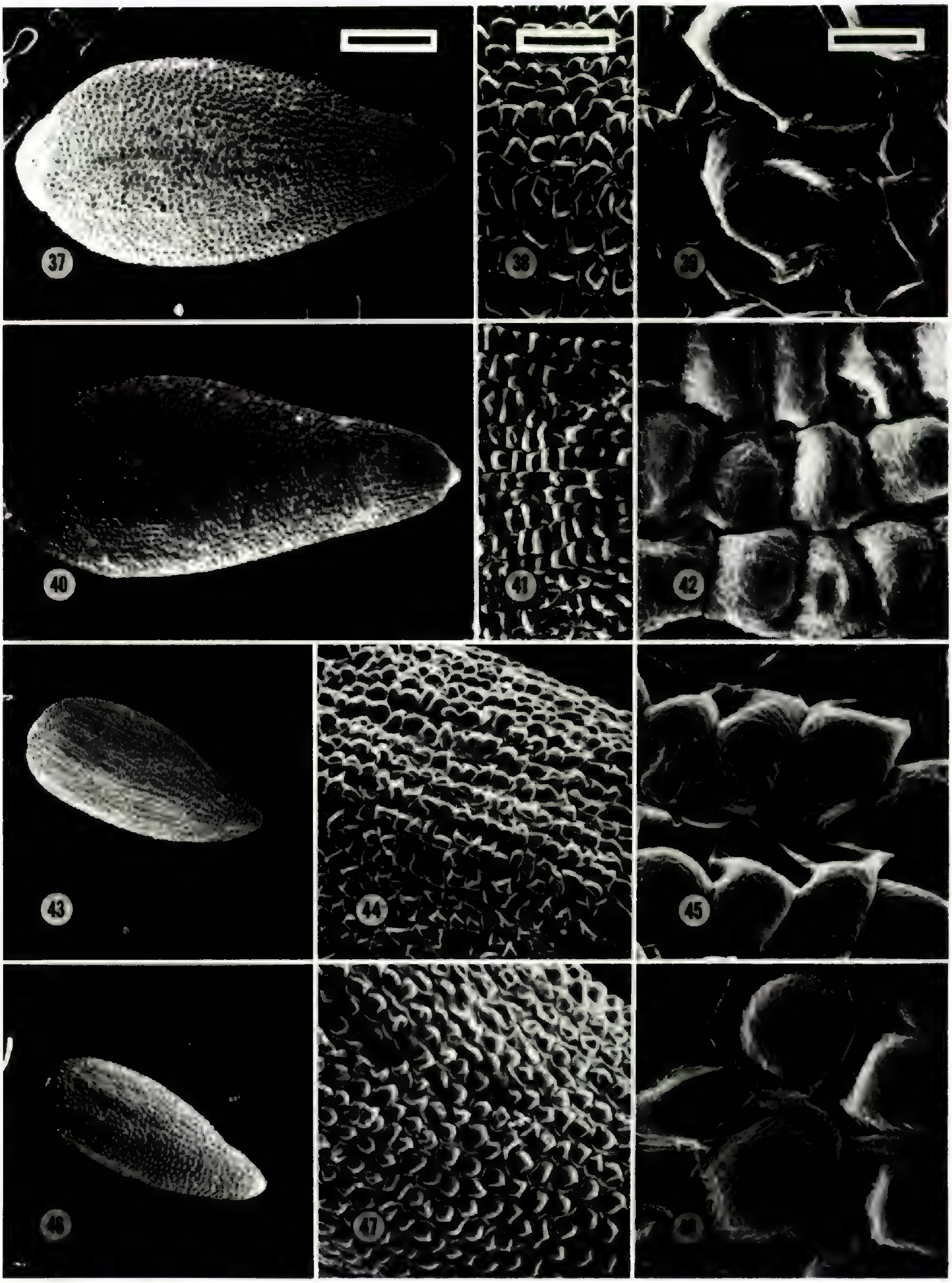
Extensive variation exists in the size, shape, and surface architecture of the species of this large section. Representatives of the species with the largest seeds, *E. rigidum* (Figs. 37–39, 40–42), may possess a prominent (Fig. 37) or relatively obscure (Fig. 40) constriction toward the micropylar end, resembling those of sect. *Cordylophorum*. The surface cells of this species are convex over most of their surface, and the radial walls are mostly obscured (Figs. 39, 42).



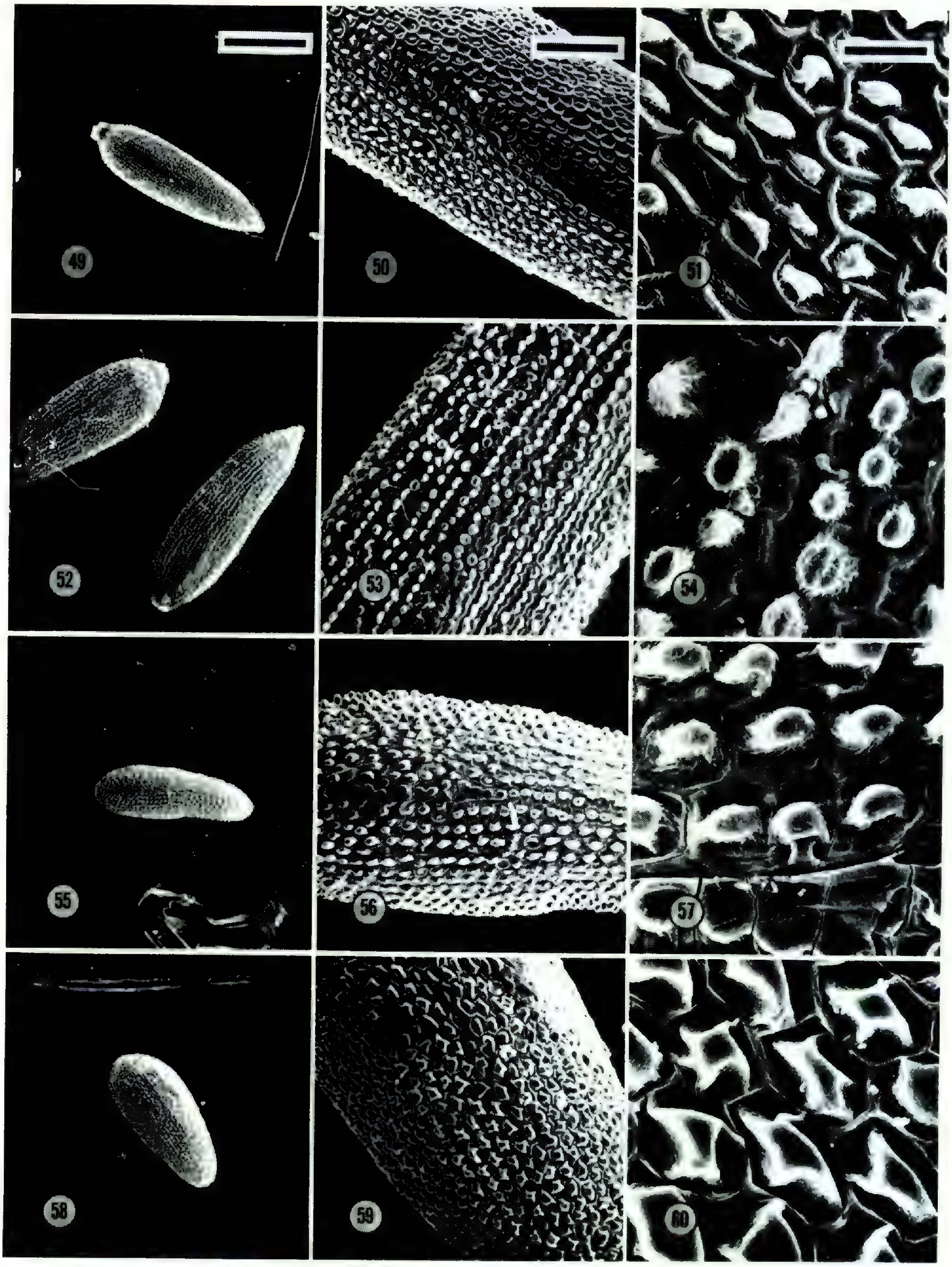
FIGURES 13–24. Scanning electron micrographs of seeds of *Epilobium* sect. *Zauschneria*. —13–15. *E. canum* subsp. *garrettii*.—16–18. *E. canum* subsp. *canum*.—19–21. *E. canum* subsp. *septentrionale*.—22–24. *E. canum* subsp. *latifolium*.



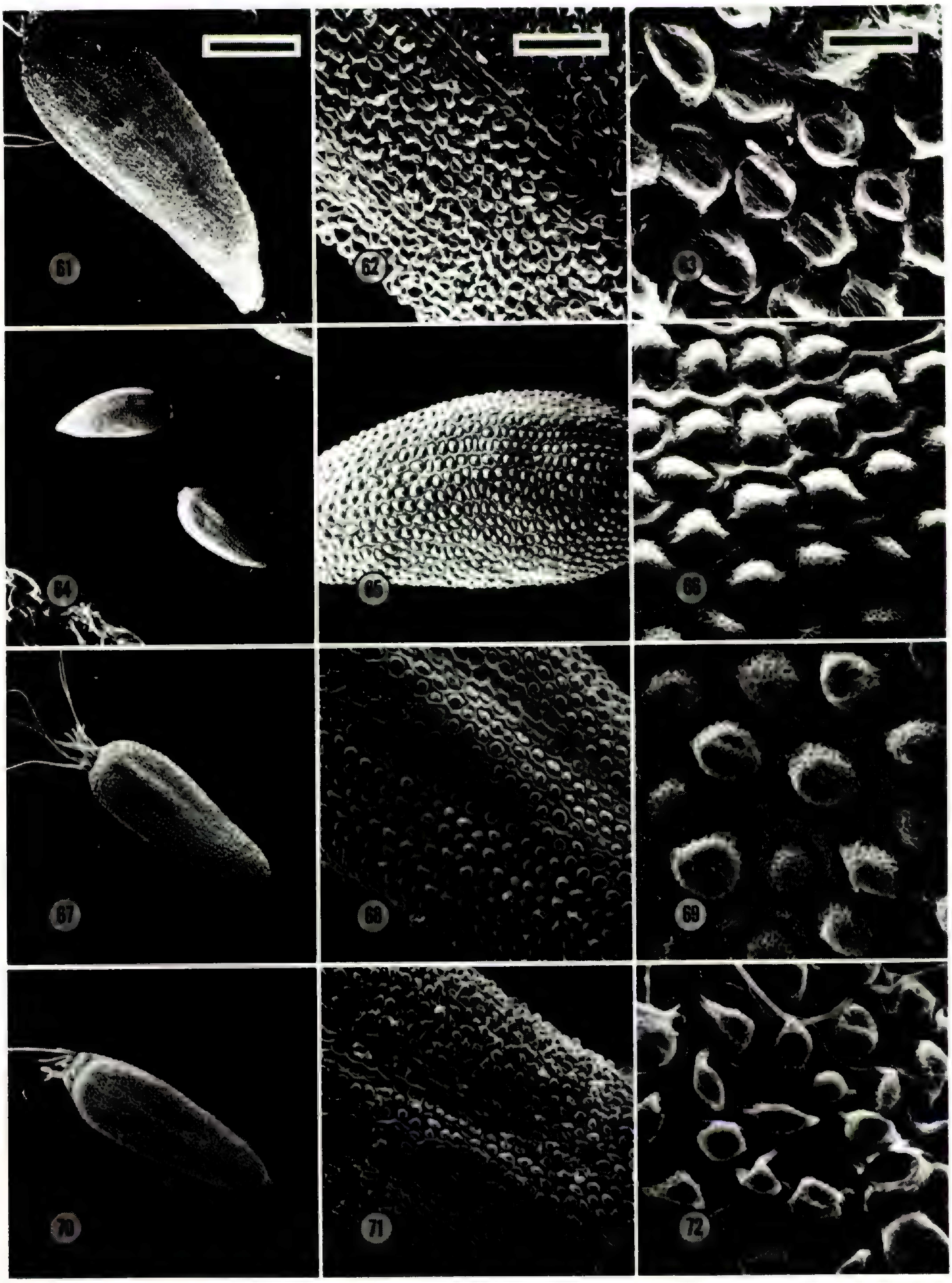
FIGURES 25–36. Scanning electron micrographs of seeds of *Epilobium* sect. *Chamaenerion*. —25–27. *E. angustifolium*.—28–30. *E. latifolium*.—31–33. *E. stevenii*.—34–36. *E. dodonaei*. The first two species belong to subsect. *Leiostylae*, the second two to subsect. *Rosmarinifolium*.



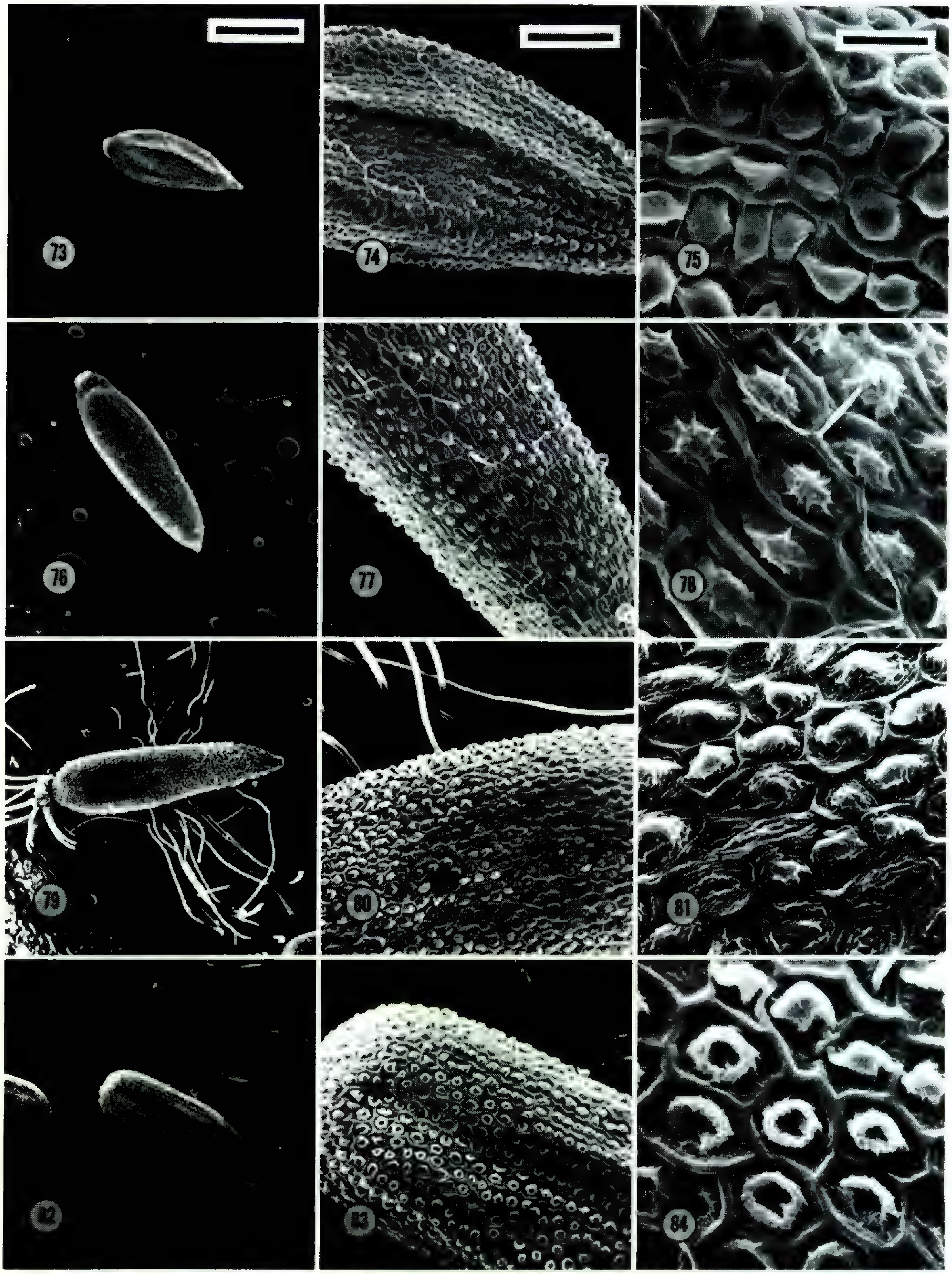
FIGURES 37–48. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*. —37–39. *E. rigidum*, *Seavey 1116*.—40–42. *E. rigidum*, *Curtis 1*.—43–45. *E. obcordatum* subsp. *obcordatum*.—46–48. *E. obcordatum* subsp. *siskiyouense*.



FIGURES 49–60. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—49–51. *E. shiroumense*.—52–54. *E. fauriei*.—55–57. *E. platystigmatosum*.—58–60. *E. stereophyllum*.



FIGURES 61–72. Scanning electron micrographs of South American species of *Epilobium* sect. *Epilobium*.—61–63. *E.* cf. *pauciflorum*.—64–66. *E. denticulatum*.—67–69. *E. glaucum*. —70–72. *E.* sp.



FIGURES 73–84. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*. —73–75. *E. hirtum*.—76–78. *E. oregonense*.—79–81. *E. coloratum*.—82–84. *E. leiophyllum*.

This combination of characters is unique in sect. *Epilobium*. The seeds of *E. obcordatum* (Figs. 43–45, 46–48) are similar in surface relief (esp. Fig. 45), but they are smaller and lack a prominent constriction at the micropylar end.

The remaining species of sect. *Epilobium* have seeds which are smaller, lack

a micropylar constriction, and are characterized by surface cells which, although often convex, always have clearly evident radial walls.

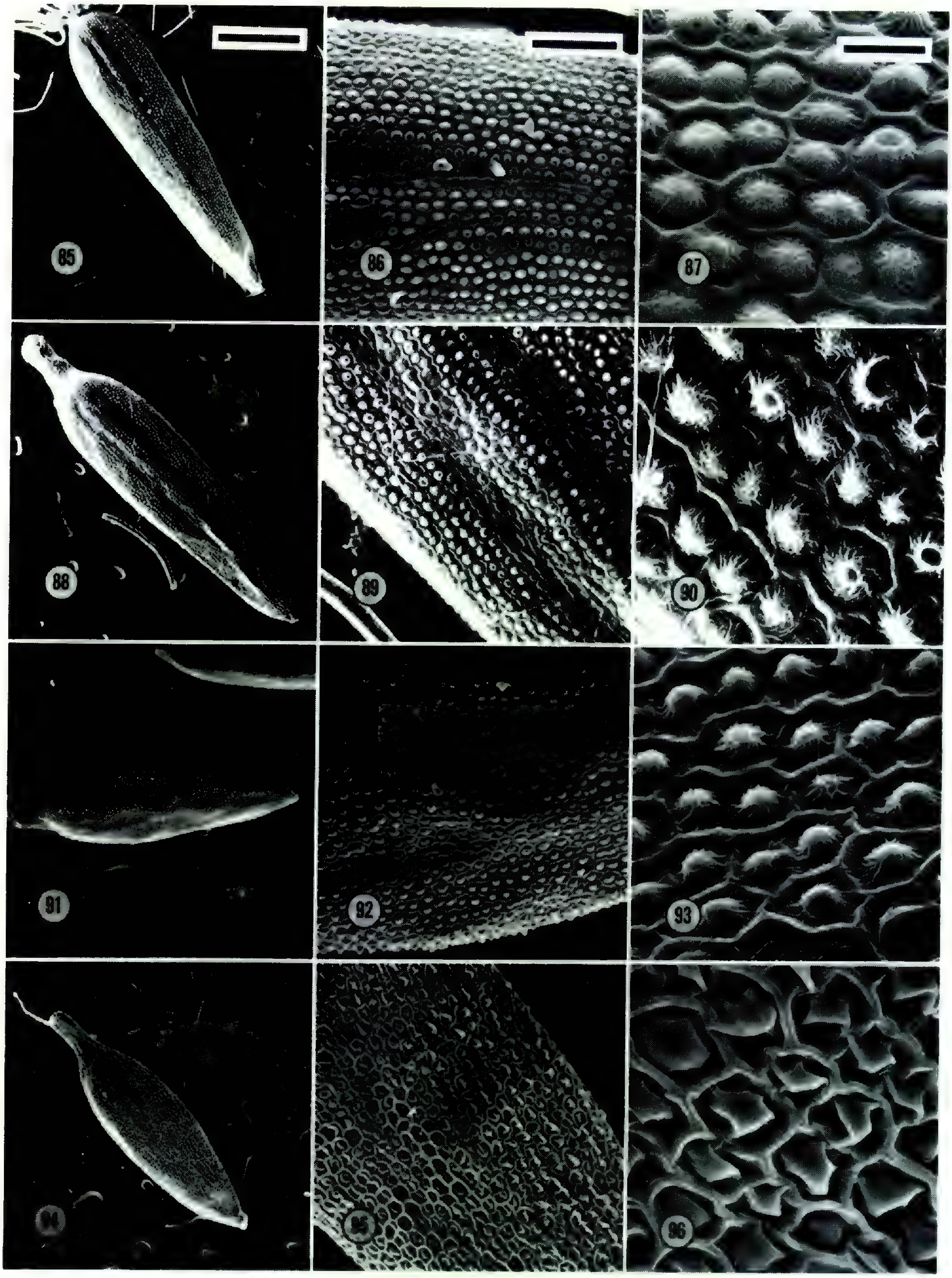
The range in size of this remaining group of species extends from approximately 0.5 mm long for *E. denticulatum* (Figs. 64–66), *E. komarovianum* (Figs. 121–123), and *E. pictum* (Figs. 124–126) to approximately 1.5 mm for *E.* cf. *pauciflorum* (Figs. 61–63), *E. pylaieanum* (Figs. 88–90), and *E. strictum* (Figs. 85–87). The range in shape of this group of species extends from the obovoid seeds of *E. hirsutum* (Figs. 112–114) and *E. obscurum* (Figs. 109–111) to the narrowly obovoid seeds of *E. strictum* (Figs. 85–87) and *E. shiroumense* (Figs. 49–51). In overall shape, *E. gunnianum* (Figs. 118–120) stands out as having an extended, flat ventral surface which extends beyond the outline of the main body of the seed.

In many species the cells in the region of attachment of the coma proliferate to varying degrees, thus forming a distinct neck. This neck is clearly evident in dorsal view in *E. alsinifolium* (Figs. 145–147), *E. anagallidifolium* (Figs. 148–150), *E. atlanticum* (Figs. 127–129), *E. chilense* (Figs. 172–174), *E. ciliatum* (Figs. 169–171), *E. denticulatum* (Figs. 64–66), *E. hirtum* (Figs. 73–75), *E. hornemannii* (Figs. 136–138), *E. oreganum* (Figs. 160–162), *E. oregonense* (Figs. 76–78), *E. scalare* (Figs. 154–156), and *E. shiroumense* (Figs. 49–51). This neck may exceed 0.2 mm in *E. davuricum* (Figs. 94–96) and *E. pylaieanum* (Figs. 88–90). Although the neck may not be seen as a distinct region in some species when viewed from directly above with the seed lying flat, it can be discerned if the seed is tilted (e.g., *E. watsonii*, Figs. 157, 202).

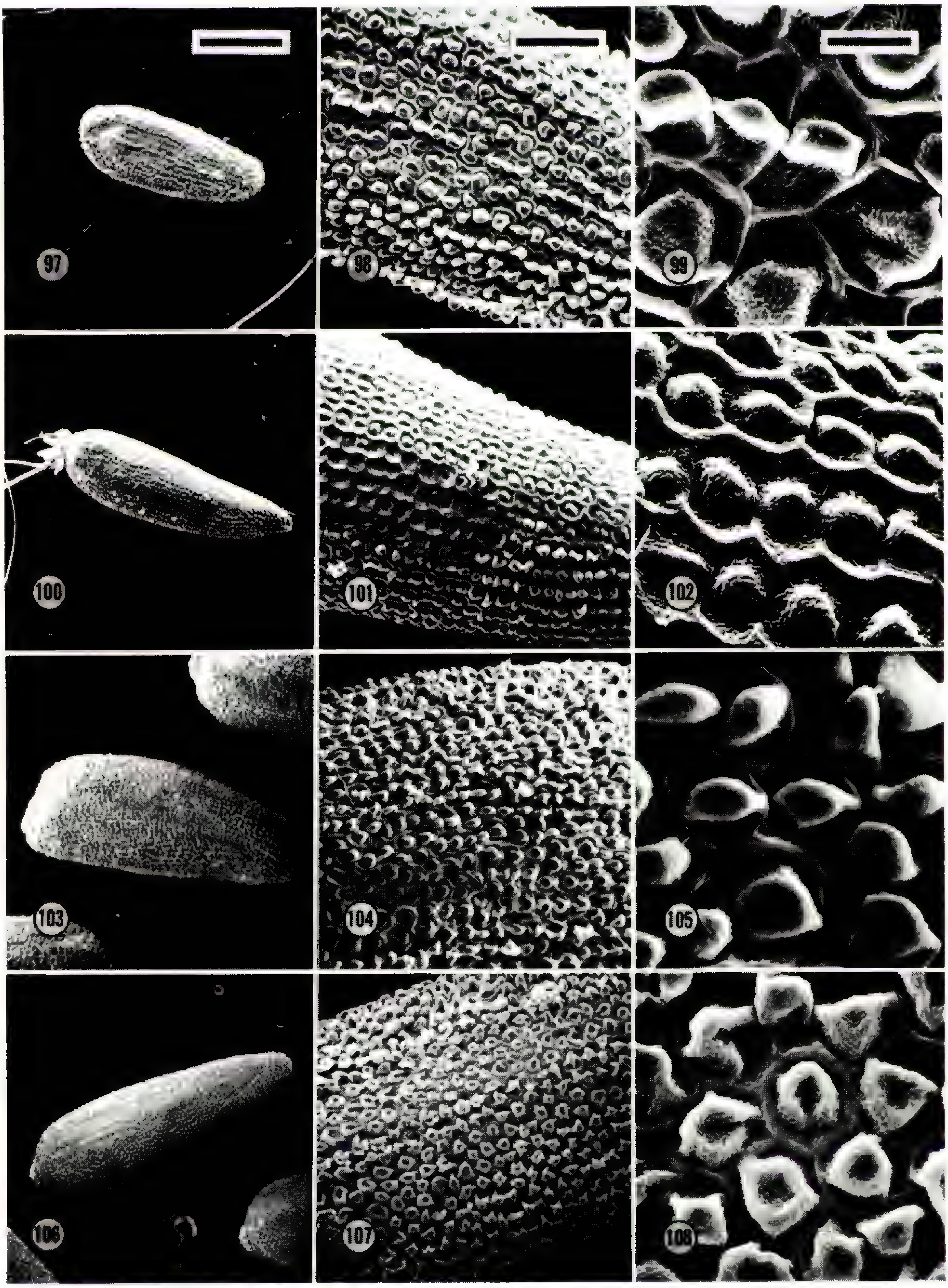
The neck region may be a moderately thick extension of the chalazal end cells (e.g., *E. strictum*, Fig. 203; *E. exaltatum*, Fig. 205) or it may be relatively thin, in which case it is displaced toward the ventral side (e.g., *E. anagallidifolium*, Fig. 204; *E. oregonense*, Fig. 206; *E. scalare*, Fig. 207). In species with the longest necks, the neck cells appear individually elongated (e.g., *E. davuricum*, Fig. 208). The individual trichomes of the coma are usually inserted at the very apex of the neck, although they are occasionally inserted over a broader area (e.g., *E. palustre*, Fig. 210). If the neck is relatively thin, as in *E. exaltatum* (Fig. 205) or *E. watsonii* (Fig. 202), it is sometimes pellucid.

There are three types of surface cells in sect. *Epilobium*: *papillose* (Group I; Berggren, 1974), cells with a convex portion centrally located on the tangential wall, variously shaped and isolated from its neighboring cells by a prominent radial wall reticulum; *foveolate* (Denford & Karas, 1974; Group III; Berggren, 1974), cells lacking any prominent feature other than the raised, regularly polygonal radial walls; and *ridged* (Group II; Berggren, 1974), cells with a centrally located convex portion which is laterally compressed and fused with the raised portions of neighboring cells, forming longitudinal ridges along the length of the seed.

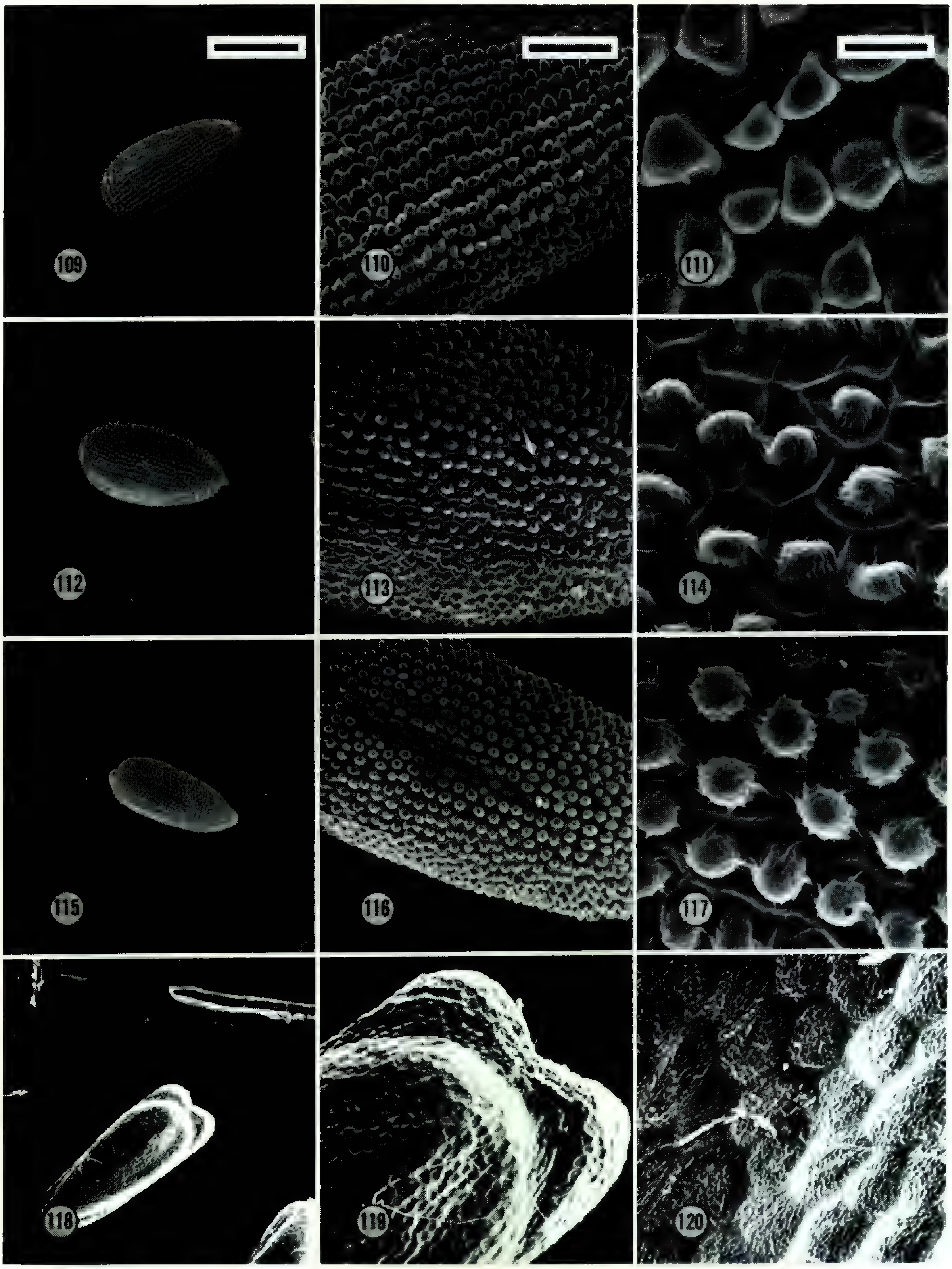
Most species of sect. *Epilobium* have papillose seeds. The central papilla of the surface cells of many species is irregularly compressed into a multisided prominence as in *E. alpestre* (Figs. 103–105), *E. amurense* (Figs. 97–99), *E. obscurum* (Figs. 109–111), *E. shiroumense* (Figs. 49–51), and *E. stereophyllum*



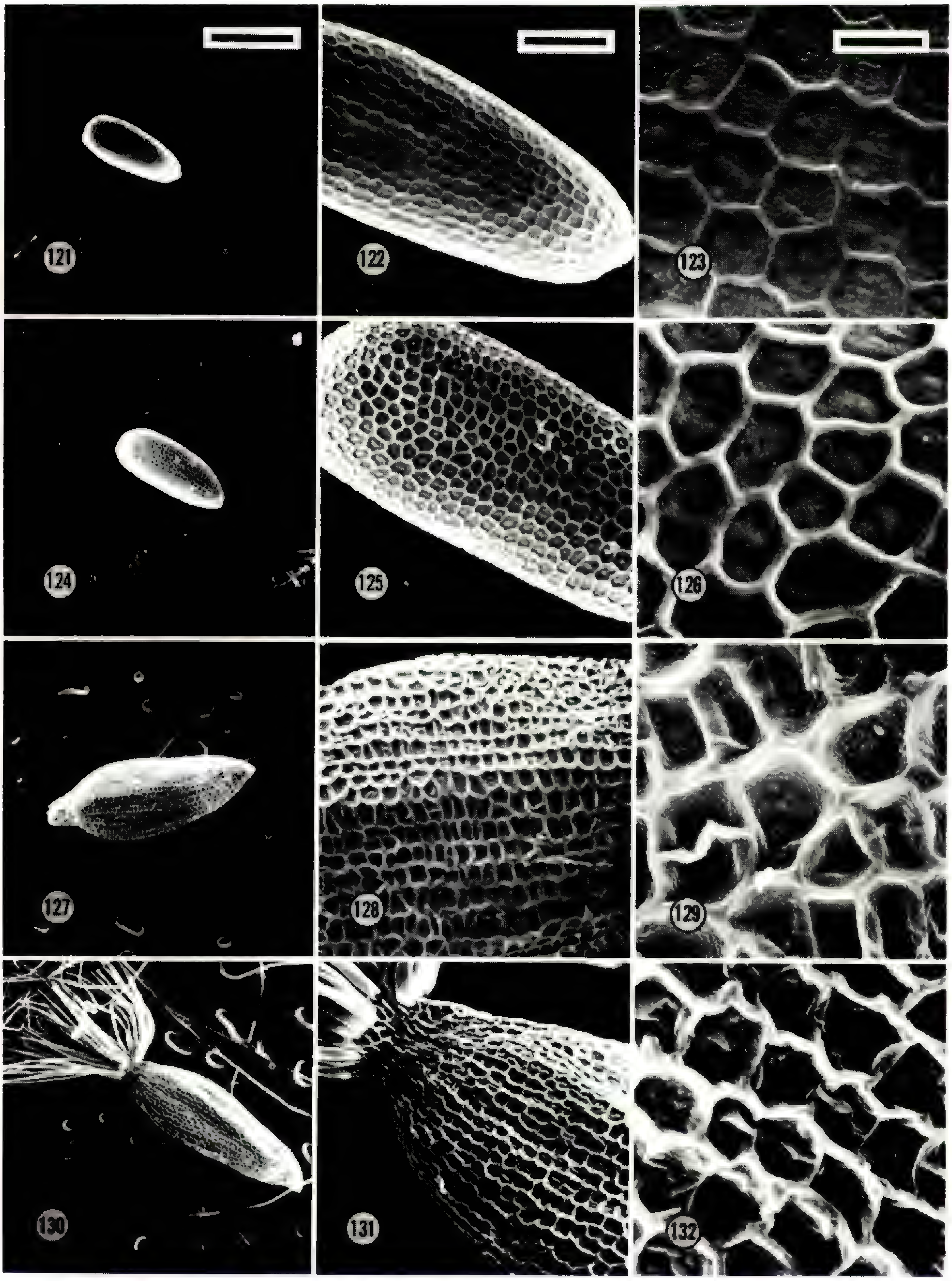
FIGURES 85–96. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*. —85–87. *E. strictum*.—88–90. *E. pylaieanum*.—91–93. *E. davuricum*, *Porsild 306*.—94–96. *E. davuricum*, *Yurtsev & Raszhivin in 1972*.



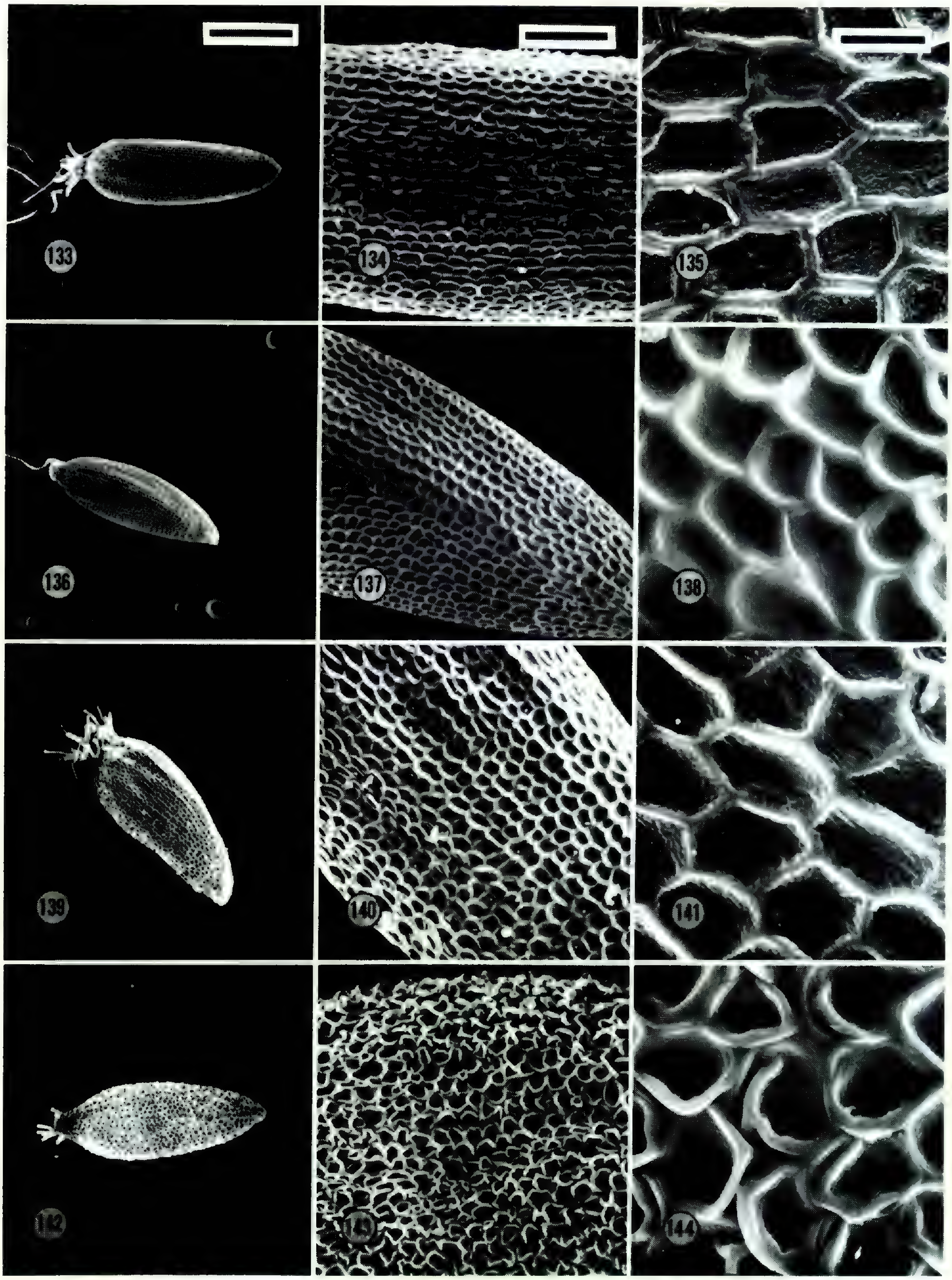
FIGURES 97–108. Scanning electron micrographs of seeds of Eurasian species of *Epilobium* sect. *Epilobium*.—97–99. *E. amurense*.—100–102. *E. pyrricholophum*.—103–105. *E. alpestre*.—106–108. *E. duriaei*.



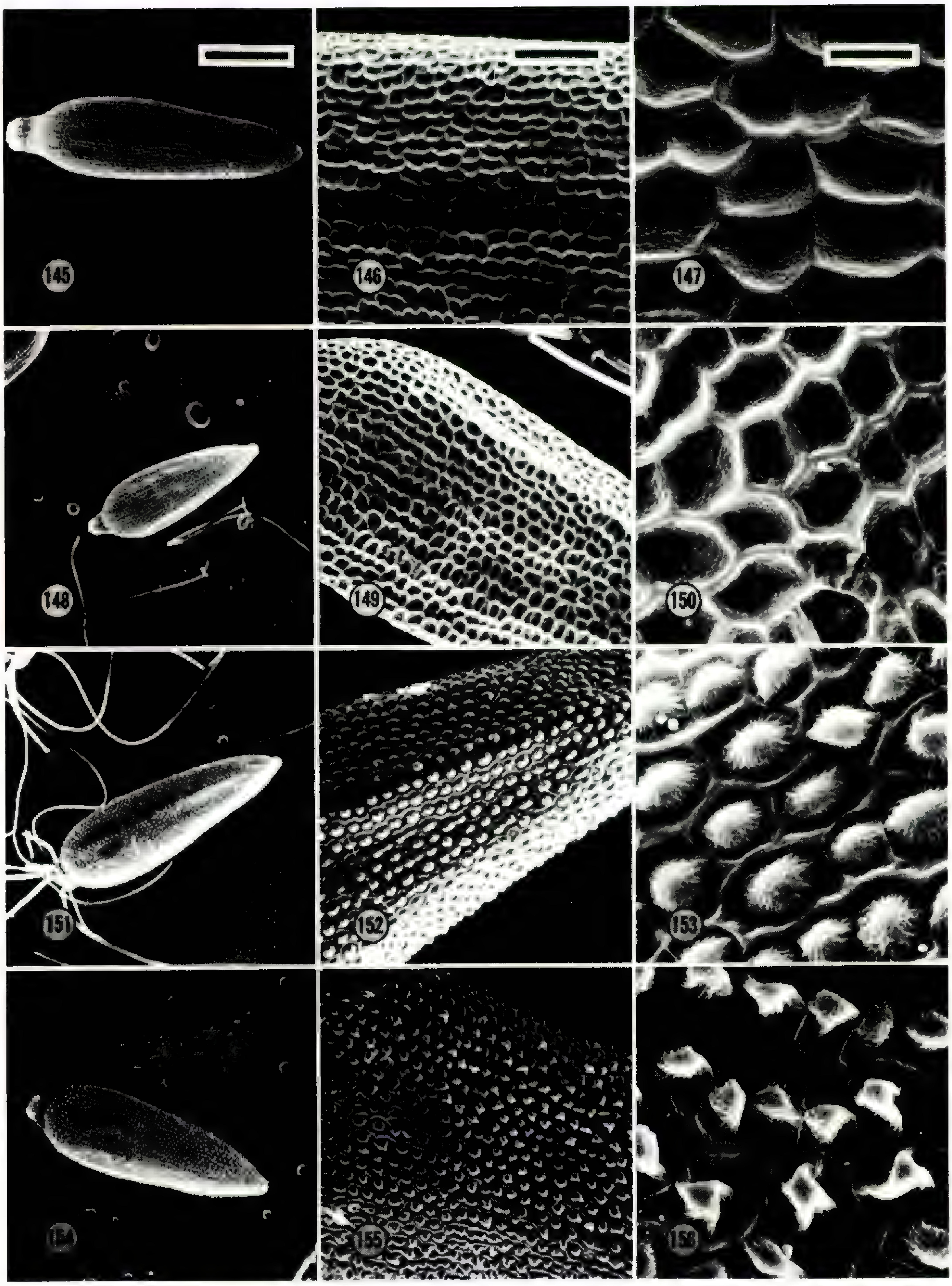
FIGURES 109–120. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*. —109–111. *E. obscurum*.—112–114. *E. hirsutum*.—115–117. *E. billardierianum* subsp. *billardierianum*.—118–120. *E. gunnianum*.



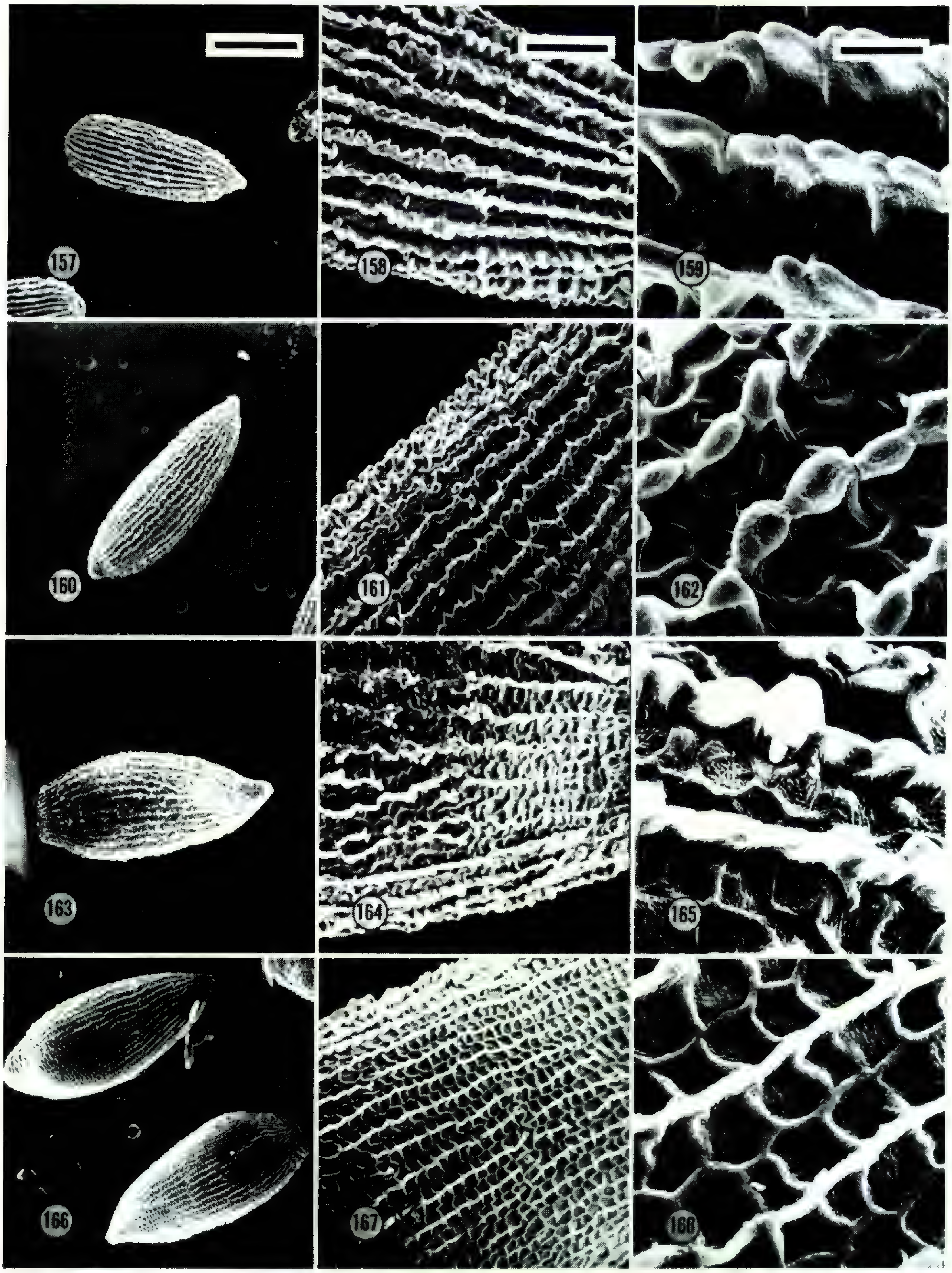
FIGURES 121–132. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*.—121–123. *E. komarovianum*.—124–126. *E. pictum*.—127–129. *E. atlanticum*.—130–132. *E. nutans*.



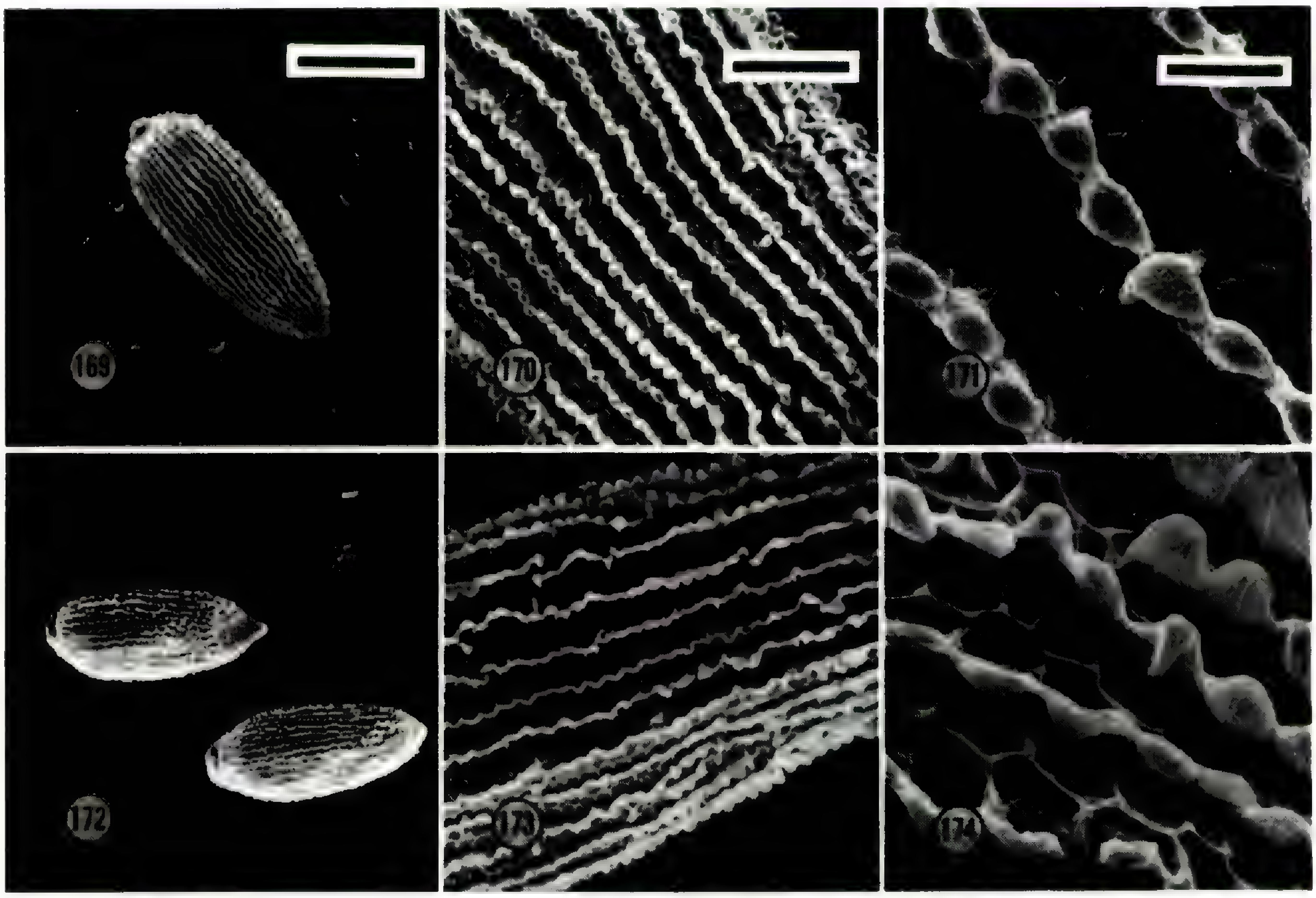
FIGURES 133–144. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*. —133–135. *E. behringianum*.—136–138. *E. hornemannii* s. lat.—139–141. *E. luteum*.—142–144. *E. treleasianum*.



FIGURES 145–156. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*. —145–147. *E. alsinifolium*.—148–150. *E. anagallidifolium*.—151–153. *E. nesophilum*.—154–156. *E. scalare*.



FIGURES 157–168. Scanning electron micrographs of seeds of North American species of *Epilobium* sect. *Epilobium*.—157–159. *E. watsonii*.—160–162. *E. oreganum*.—163–165. *E. exaltatum, M409*.—166–168. *E. exaltatum, M559*.

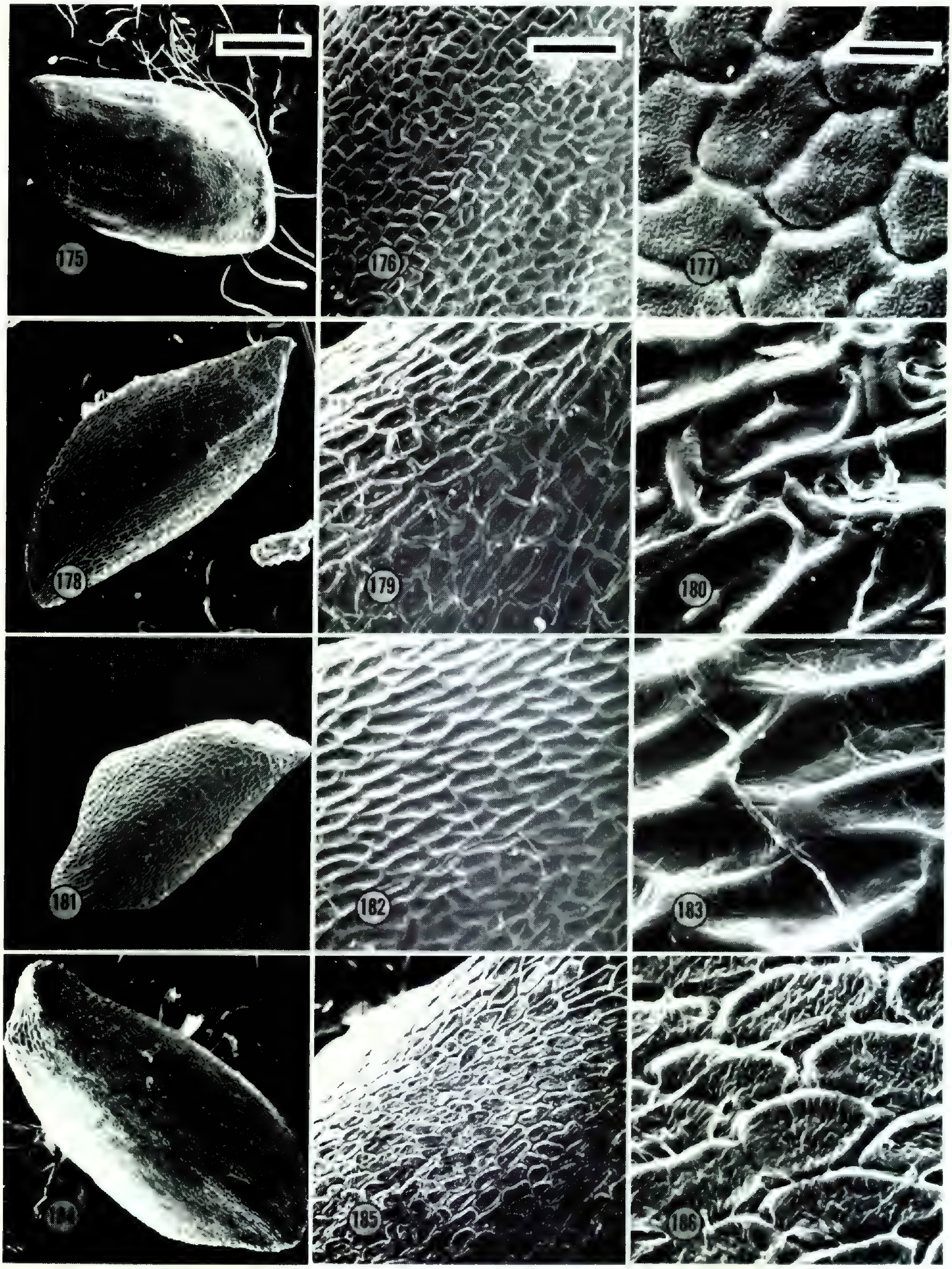


FIGURES 169–174. Scanning electron micrographs of seeds of *Epilobium* sect. *Epilobium*. —169–171. *E. ciliatum*.—172–174. *E. chilense*.

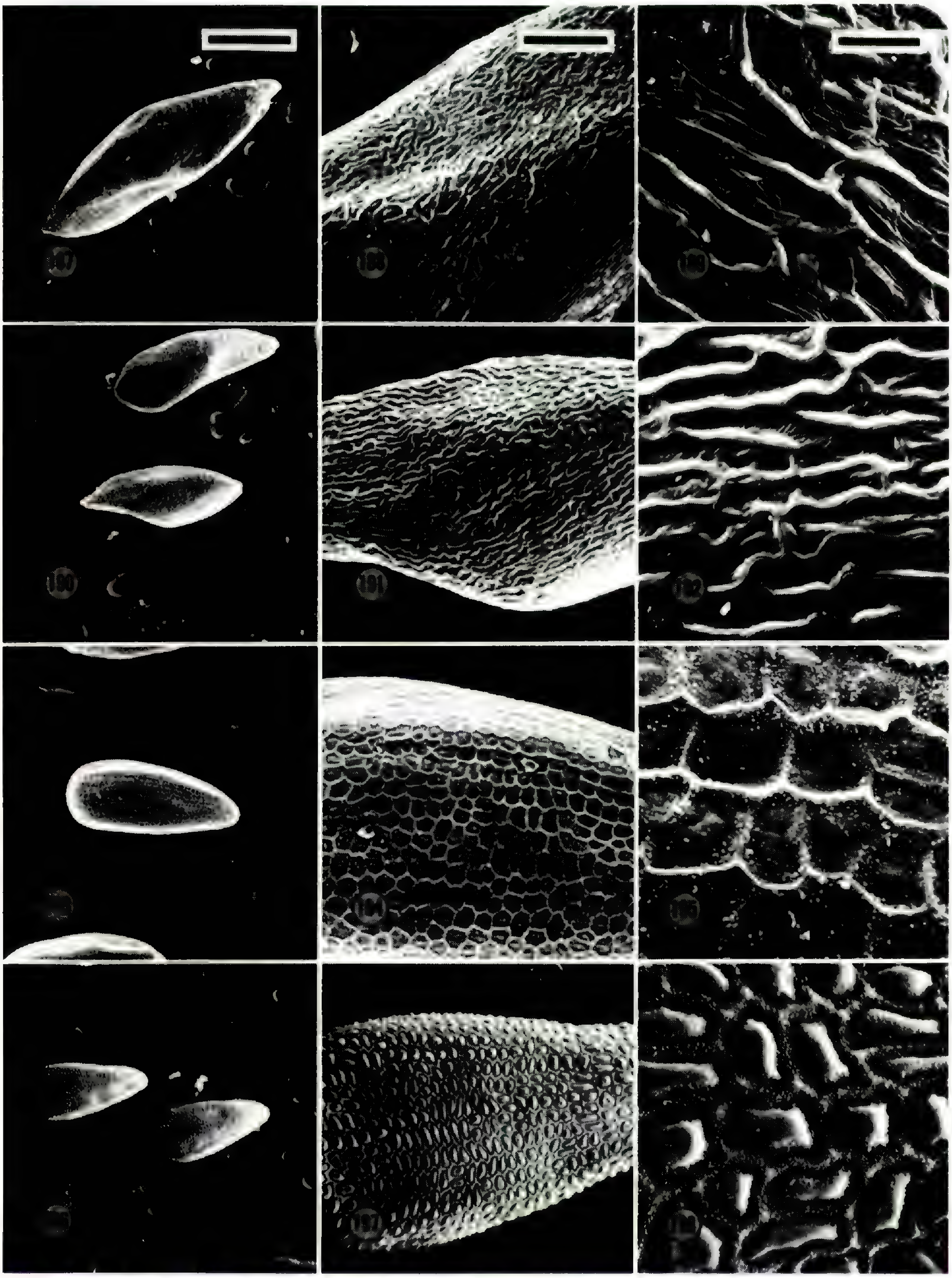
(Figs. 58–60), whereas in others it remains more regularly domeshaped, as in *E. denticulatum* (Figs. 64–66), *E. fauriei* (Figs. 52–54), *E. glaucum* (Figs. 67–69), and *E. pyrricholophum* (Figs. 100–102). In some species, the papilla is marked by radial lines which appear as fine ridges, as in *E. oregonense* (Figs. 76–78), *E. pylaieanum* (Figs. 88–90), some samples of *E. billardierianum* (Figs. 115–117), *E. davuricum* (Figs. 91–93), *E. hirsutum* (Figs. 112–114), and *E. nesophilum* (Figs. 151–153). The papilla of some species, such as *E. leiophyllum* (Figs. 82–84) and *E. duriaei* (Figs. 106–108), is collapsed in the center. The surface cells are usually arranged in irregular rows running longitudinally the length of the seed, but in some species, such as *E. amurense* (Figs. 97–99), *E. fauriei* (Figs. 52–54), and *E. obscurum* (Figs. 109–111), the rows are distinctly regularly arranged.

In foveolate seeds the regularly polygonal reticulum formed by the radial walls is the most prominent feature of the seed surface. This radial wall reticulum is relatively low on the seeds of *E. gunnianum* (Figs. 118–120), and *E. komarovianum* (Figs. 121–123), but more pronounced on the seeds of *E. alsinifolium* (Figs. 146–147), *E. anagallidifolium* (Figs. 148–150), *E. atlanticum* (Figs. 127–129), *E. behringianum* (Figs. 133–135), *E. hornemannii* (Figs. 136–138), *E. luteum* (Figs. 139–141), *E. nutans* (Figs. 130–132), and *E. pictum* (Figs. 124–126).

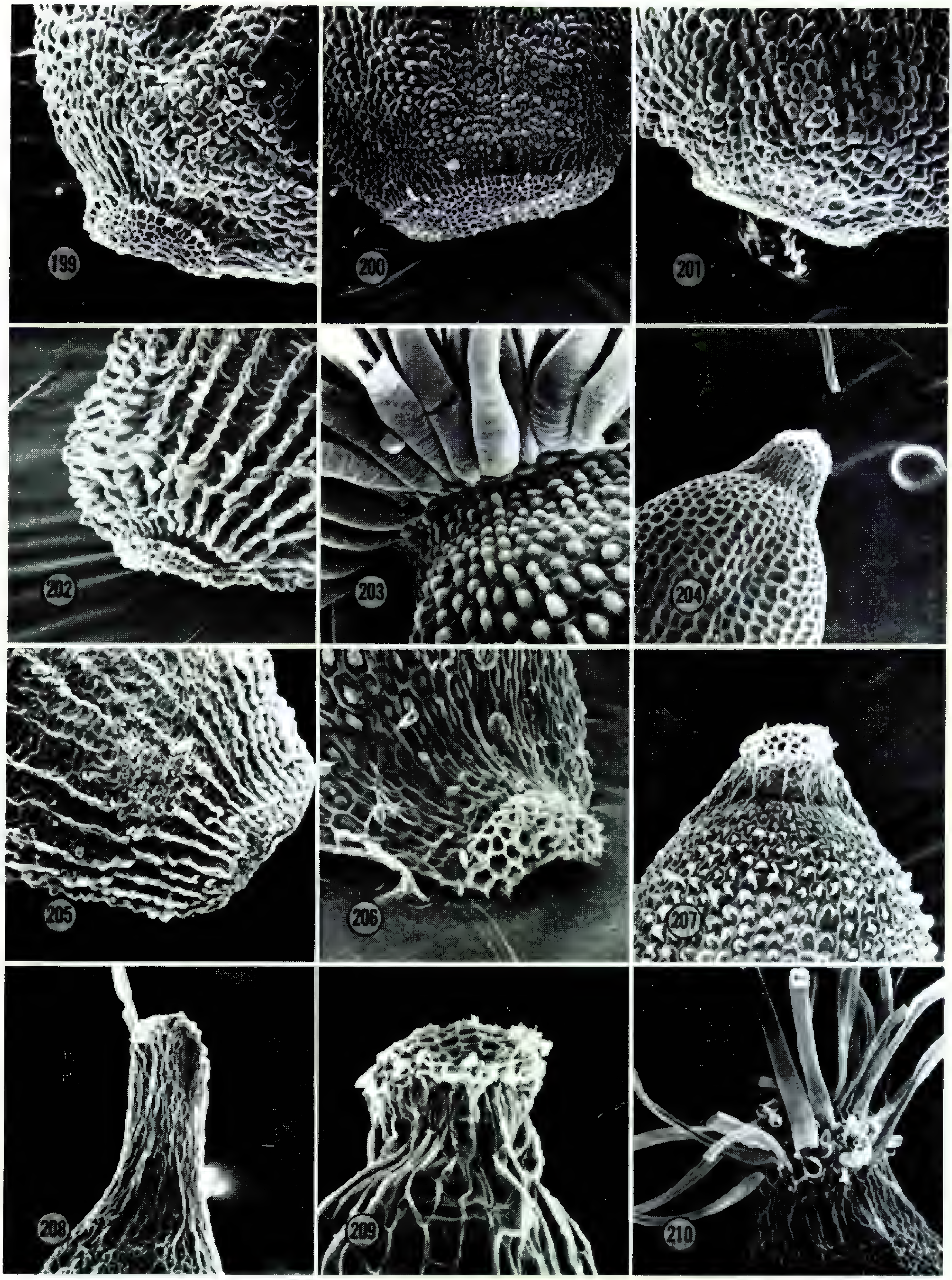
Ridged seeds, marked by longitudinal rows of laterally compressed, fused ridges, are found principally in North American species. Among these are *E. ciliatum* (Figs. 169–171), *E. exaltatum* (Figs. 163–165), *E. oreganum* (Figs. 160–162), and *E. watsonii* (Figs. 157–159). The South American *E. chilense*



FIGURES 175–186. Scanning electron micrographs of seeds of the four species of *Boisduvalia* sect. *Boisduvalia*.—175–177. *B. densiflora*.—178–180. *B. macrantha*.—181–183. *B. stricta*.—184–186. *B. subulata*.



FIGURES 187–198. Scanning electron micrographs of seeds of the species of *Boisduvalia* sect. *Currania* and *Epilobium* sect. *Crossostigma*.—187–189. *Boisduvalia cleistogama*.—190–192. *B. glabella*.—193–195. *Epilobium minutum*.—196–198. *E. foliosum*.



FIGURES 199–210. Scanning electron micrographs showing variation in chalazal end of seeds of *Epilobium*, including the development of more or less pronounced beaks. All taxa are members of sect. *Epilobium* except as indicated in parentheses following their names.—199. *Epilobium canum* subsp. *canum* (*Zauschneria*).—200. *E. rigidum*, *Curtis 1*.—201. *E. obcordatum* subsp. *obcordatum*.—202. *E. watsonii*.—203. *E. strictum*.—204. *E. anagallidifolium*.—205. *E. exaltatum*.—206. *E. oregonense*.—207. *E. scalare*.—208. *E. davuricum*, *Yurtsev & Raszhivin in 1972*.—209. *E. angustifolium*.—210. *E. palustre*.

(Figs. 172–174) likewise has ridged seeds. The seeds of hybrids between species with ridged and papillose seeds are intermediate in various ways and have been illustrated by Skvortsov & Rusanovich (1973).

II. *Boisduvalia*

The seeds of *Boisduvalia* are distinct from those of *Epilobium*. Their shape, which is irregularly angular-fusiform, is unique, as is the structure of their surface cells. The relatively broad seeds of *B. densiflora* (Figs. 175–177) and *B. subulata* (Figs. 184–196) have surface cells which are slightly raised, flat, and irregularly polygonal. The seeds of *B. macrantha* (Figs. 178–180), *B. stricta* (Figs. 181–183), and the narrower seeds of *B. cleistogama* (Figs. 187–189) and *B. glabella* (Figs. 190–192), have surfaces that are covered by an irregularly striated reticulum composed of the unevenly joining radial walls of the surface cells.

Discussion

A number of distinct seed types occur in the genera *Boisduvalia* and *Epilobium*, as will be discussed below. In both genera, as in other Onagraceae, the surface architecture is made up of the regularly repeated structures of individual surface cells. The characteristic forms of these surface cells are the result of differential thickening in their walls, as thin sections of the seeds of *Epilobium* (Kytövuori, 1972; Denford & Karas, 1974) demonstrate; seed coat patterns in many other genera are comparable, for example in *Cordylanthus* (Chuang & Heckard, 1972), Melastomataceae (Whiffin & Tomb, 1972), and *Mentzelia* (Hill, 1976), as well as other investigations reviewed by Brisson & Peterson (1976).

There is a major contrast in Epilobieae between the angular-prismatic seeds of *Boisduvalia*, which lack a coma, and the regularly obovoid, flattened ones of *Epilobium*, which have a coma in all taxa except in a few in which it has been lost. In addition, the surface cells in *Boisduvalia* are irregular and thus unlike any found in *Epilobium*. Those of *B. densiflora* ($n = 10$) and *B. subulata* ($n = 19$) are low, flat, and irregularly polygonal, whereas those of *B. macrantha* ($n = 10$) and its probable aneuploid derivative *B. stricta* ($n = 9$; Raven & Moore, 1965) are concave and have radial walls that are longitudinally striate and irregularly thickened. These four species comprise sect. *Boisduvalia* (Raven, 1976); the remaining two species, which comprise sect. *Currania* ($n = 15$), have seeds that resemble those of *B. macrantha* and *B. stricta*, although they are smaller.

In *Epilobium*, it is convenient to recognize seven distinct types of seeds, and these will be discussed in turn.

1. Large, obovoid, constricted. In sects. *Cordylophorum*, *Xerolobium*, and *Zauschneria*, the seeds are obovoid, large, and more or less prominently constricted toward the micropylar end. Their surface is made up of cells which are smooth and convex, with obscure lateral walls (Figs. 1–24). The relatively prominent side walls in our preparation of *E. canum* subsp. *canum* probably are associated with shrivelling. The five species that comprise these three sections are

relictual (Raven, 1976), and this seed type is almost certainly primitive for *Epilobium*. In sect. *Epilobium*, with some 185 species and a worldwide distribution, it occurs only in *E. rigidum* (Figs. 37–39, 40–42), a large-flowered, xerophytic species of the Siskiyou Mountains of northwestern California and adjacent Oregon. The Siskiyou Mountains are a well known relict area (Whittaker, 1960), and *E. rigidum* very likely resembles the basic stock from which the remaining species of sect. *Epilobium* have diverged. As in *E. nevadense, E. nivium,* and *E. paniculatum*, the subtending bracts in *E. rigidum* are fused to their pedicel in all but the lowermost flowers. The phylogenetic significance of this observation remains to be determined.

2. Papillose. Most species of sect. *Epilobium* have seeds that are smaller, papillose, obovoid to narrowly obovoid, and lack a micropylar constriction. The lateral walls of their surface cells are prominent. These include *E. obcordatum* (Figs. 43–45, 46–48), the species most closely related to *E. rigidum* and, like it, a large-flowered xerophyte of the western United States. In addition, the four species of sect. *Chamaenerion* subsect. *Rosmarinifolium*, exemplified by *E. dodonaei* (Figs. 34–36) and *E. stevenii* (Figs. 31–33), have this seed type. It seems clearly to have evolved from the first type and to have given rise in turn to all of the other more specialized seed types within the genus, with the probable exception of that found in sect. *Crossostigma*. The tribe Epilobieae seems to have consisted initially of xerophytes, from which the more widespread and numerous mesophytic and hydrophytic species were derived. Perhaps an evolutionary trend toward more numerous, smaller seeds accompanied the exploitation of such habitats.

Seeds of this type characterize more than a hundred species, including the European *E. alpestre, E. collinum, E. duriaei, E. hirsutum, E. lanceolatum, E. montanum, E. nervosum, E. obscurum, E. parviflorum, E. roseum,* and *E. tetragonum*, as well as the circumboreal *E. davuricum* and *E. palustre* (Skvortsov & Rusanovitch, 1974; Berggren, 1974; this paper). Papillose seeds also occur in the Asian *E. amurense*, (Figs. 97–99), *E. fauriei* (Figs. 52–54), *E. platystigmatosum* (Figs. 55–57) and *E. pyrricholophum* (Figs. 100–102); the South American *E. denticulatum* (Figs. 64–66), *E. glaucum* (Figs. 67–69), *E. hirtum* (Figs. 73–75), *E.* cf. *pauciflorum* (Figs. 61–63), and one unidentified species (South American species # 1, Figs. 70–72); the African *E. stereophyllum* (Figs. 58–60); the Australasian *E. billardierianum* (Figs. 115–117); and the North American *E. coloratum* (Figs. 79–81), *E. oregonense* (Figs. 76–78), *E. pylaieanum* (Figs. 88–90), and *E. strictum* (Figs. 85–87), as well as most populations of *E. saximontanum* Hausskn. Although only one Australasian species of this first type of surface structure is illustrated in this paper, most species of this region have seeds of this type (Raven & Raven, 1976).

Many of the microstructural details of papillose seeds are strikingly constant from one sample to another. The convex portion of the surface cells of *E. hirsutum* (Figs. 112–114), for example, are characterized by spirally arranged radial lines, as illustrated by Skvortsov & Rusanovitch (1974; fig. 1C). Similarly, the surface cells of *E. nesophilum* (Figs. 151–153), and the closely related *E. pylaieanum* (Figs. 88–90) and *E. davuricum* (Figs. 91–93) have characteristically

low convex tangential walls with radial lines as illustrated in Skvortsov & Rusanovitch (1974: figs. 2E, F, and fig. 2G, respectively), although considerable variability in surface structure within these two species is also evident in both studies (e.g., *E. davuricum*, Figs. 91–93, 94–96).

Nearly all of the species with papillose seeds in sect. *Epilobium*, well over a hundred, have the BB chromosome arrangement (Seavey & Raven, 1976; unpublished). Among the exceptions are the Asian *E. fauriei*, *E. platystigmatosum*, and *E. shiroumense*, as well as most populations of the circumboreal *E. hornemannii* s. lat. and the North American *E. clavatum* Trel., all of which have the CC arrangement. In addition, some of the species with the AA chromosome arrangement, including the South American species of the group *Denticulata* (Samuelsson, 1923, 1930) and the North American *E. glaberrimum* Barbey and *E. brevistylum* Barbey, as well as *E. saximontanum*, also have papillose seeds. Both the AA and CC chromosome arrangements differ from BB by one reciprocal translocation, and we believe that each may be independently derived from BB. On the basis of the evidence presented here, it appears that the common ancestor of each of these groups had papillose seeds.

Most species of Haussknecht's (1884) group *Palustriformes*, including *E. davuricum* (Figs. 91–93, 94–96, 208), *E. palustre* (Fig. 210), and *E. pylaieanum* (Figs. 88–90) among those illustrated in the present study, have an exaggerated beak at the chalazal end of the seed; although others, such as *E. strictum*, which undoubtedly belongs to this group, do not (Figs. 85–87, 203). The *Palustriformes* have the BB chromosome arrangement and papillose seeds in all taxa; similar in these respects is *E. oregonense* (Figs. 76–78). *Epilobium scalare*, a Newfoundland endemic that has been collected only once, has papillose seeds and a prominent beak also but does not resemble *Palustriformes* in most respects. Chalazal beaks are discussed in general on p. 30 and illustrated in Figs. 199–210.

3. Foveolate. By flattening of the central papilla found in the surface cells of the seeds of the preceding group, foveolate seeds (Danford & Karas, 1974) have evolved. Such seeds, as viewed with a 20× lens, have usually been described as "smooth" in taxonomic papers on *Epilobium*. Some species, including the New Zealand *E. alsinoides* (different subspecies), have some populations with papillose seeds and others with foveolate seeds. The same occurs in the circumboreal *E. hornemannii* s. lat. and in the North American *E. clavatum*. It appears, therefore, that the evolution of foveolate seeds has taken place repeatedly within the genus.

In Australasia, where all species have the BB chromosome arrangement and presumably evolved from a common ancestor (Raven & Raven, 1976), 31 species have papillose seeds; 10, including *E. komarovianum* (Figs. 121–123) and *E. pictum* (Figs. 124–126) have foveolate seeds; *E. alsinoides*, already mentioned, has both papillose and foveolate seeds in different subspecies; and 4 species, including *E. gunnianum* (Figs. 118–120) have a distinctive seed type that will be discussed below. In almost every one of the 11 species in which foveolate seeds occur, these appear to have evolved separately from papillose seeds (Raven & Raven, 1976).

In North America, foveolate seeds occur in *Epilobium luteum*, a rather iso-

lated species, and in some populations of the *E. glandulosum* complex (AA). In addition, they are characteristic of some or all populations of several entities in the CC group: *E. anagallidifolium* (Figs. 148–150), *E. behringianum* (Figs. 133–135), *E. clavatum*, and *E. hornemannii* s. lat. (Figs. 136–138). The seeds of *E. treleasianum* may be papillose (Figs. 142–144) or foveolate, owing to the hybrid nature of *E. treleasianum*, a series of populations of hybrid origin between *E. luteum* (seeds foveolate) and other species (Seavey, in preparation). Papillose seeds appear to be dominant in a genetic sense over foveolate ones.

Among the species that occur in Europe, only species of the CC (*Alpinae*) group and three other species—*E. nutans* (BB in part; Figs. 130–132), *E. atlanticum* (AA; Figs. 127–129), and *E. alsinifolium* (AA; Figs. 145–147)—have foveolate seeds. Judged from the wide morphological gap between the latter two species and the different chromosome arrangement in the first, it is likely that all evolved foveolate seeds independently. The fact that all three are species of low stature that occur in alpine habitats, like the species of group *Alpinae* (here defined to comprise only CC species and therefore to exclude *E. alsinifolium*), suggests that some common selective force may favor foveolate seeds under such conditions. The third European species with the AA chromosome arrangement, *E. alpestre* (Figs. 103–105), has papillose seeds.

4. Obovoid-patelliform. Four Australasian species—*E. gunnianum* (Figs. 118–120), *E. curtisiae* Raven, *E. willisii* Raven & Engelhorn, and *E. angustum* (Cheesem.) Raven & Engelhorn—have distinctive seeds with a hollow ring around their adaxial side, which are thus patelliform. The first three are probably closely related, but the occurrence of similar seeds in *E. angustum*, apparently closely related to *E. komarovianum*, has not been explained satisfactorily (Raven & Raven, 1976). The seeds of *E. willisii* and of many populations of *E. gunnianum* are finely papillose, those of the other taxa foveolate. The obovoid-patelliform seed type undoubtedly evolved from the more frequent papillose type within Australasia.

5. Irregularly reticulate. The three species of sect. *Chamaenerion* subsect. *Leiostylae* have seeds in which the very thin radial walls of the epidermal cells of the seed coat form an irregularly polygonal reticulum (Figs. 25–30). The four other species of sect. *Chamaenerion*, comprising subsect. *Rosmarinifolium*, have papillose seeds that resemble those of most species of sect. *Epilobium* in size and shape. The close relationship of the two subsections of sect. *Chamaenerion* is beyond question in that they share the following unique or highly unusual characteristics for the genus: all leaves spirally arranged, flowers zygomorphic, floral tube obsolete, pollen shed singly. This indicates unequivocally that the unusual seeds of subsect. *Leiostylae*, stressed by Skvortsov & Rusanovitch (1974) and by Brisson & Peterson (1976) as an argument for the generic distinctness of sect. *Chamaenerion*, represent instead an evolutionary specialization within this group, otherwise characterized by seeds similar to those of many species of sect. *Epilobium*. Also implied by the seed morphology of subsect. *Rosmarinifolium* is the divergence of sect. *Chamaenerion* from an ancestor that would be placed within sect. *Epilobium* long after the divergence of sects. *Cordylophorum*, *Xerolobium*, and *Zauschneria* from species such as *E. rigidum*. Additional evidence for

the close relationship of sect. *Chamaenerion* with sect. *Epilobium* is summarized by Raven (1976).

6. Ridged. Within the North American group of species with the AA chromosome arrangement (Seavey & Raven, 1976), there has originated a distinctive seed type, described above, that doubtless delimits a phylogenetically coherent group of taxa. Illustrated here are *E. ciliatum* (Figs. 169–171; extends to Japan), *E. exaltatum* (Figs. 163–165), *E. oreganum* (Figs. 160–162), and *E. watsonii* (Figs. 157–159). *Epilobium ciliatum* occurs as an adventive in Europe and in Australasia (Raven & Raven, 1976), and its seeds have been illustrated several times (as *E. adenocaulon* Hausskn., Troughton & Donaldson, 1972: pls. 103–104; Skvortsov & Rusanovitch, 1973, 1974; Berggren, 1974; Raven & Raven, 1976). Virtually identical seeds occur in the South American *E. chilense* (Figs. 172–174), this suggesting recent immigration to South America following the origin of the group in North America. Within the *Epilobium glandulosum* complex foveolate seeds also occur, but these have probably been derived from ridged ones. The most primitive species of this group is apparently a local endemic of bogs in the Siskiyou Mountains, *E. oreganum*, which has exserted, deeply 4-lobed stigmas.

Denford & Karas (1974) have interpreted the ridges in seeds of this type as being formed of rows of flattened papillose cells flanked on both sides by foveolate cells. Our SEM observations, however, show clearly that the ridges are instead formed of the finlike central portions of individual surface cells, all such cells on the abaxial side of the seed being similar. No foveolate cells were observed on the abaxial surface of these seeds.

7. Finely papillose. The distinctive seeds of sect. *Crossostigma*, described on p. 23 and by Seavey et al. (1977), cannot easily be related to any other seed type in the genus, and the relationships of the two annual species included in this section are obscure.

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THE BIOSYSTEMATICS OF *CALYLOPHUS* (ONAGRACEAE)[1]

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ABSTRACT

The genus *Calylophus* (Onagraceae), a segregate of *Oenothera*, was studied in reference to systematic relationships, breeding systems, pollination, and cytology. Six species are recognized, four in sect. *Salpingia*: *C. tubicula*, *C. hartwegii*, *C. toumeyi* and *C. lavandulifolius*, and two in sect. *Calylophus*: *C. berlandieri* (formerly *C. drummondianus*) and *C. serrulatus*. Several changes in nomenclature and rank are made. Crosses performed among species demonstrated strong barriers to hybridization between the two sections of the genus and slight to moderate barriers among species within sections.

Populations of *Calylophus* are distributed through the Great Plains, the southwestern United States, and northern Mexico. The various taxa occupy distinct habitats which range from xeric sites in the Chihuahuan Desert to relatively mesic pine and pine-oak forests. In most forms of the genus, the plants are suffrutescent perennials and occupy calcareous soils. One form is restricted primarily to gypsum soils.

Cytological investigations showed a remarkable degree of translocation heterozygosity in natural populations of *Calylophus*. Translocations were observed in all taxa, with 75% of 183 plants (excluding *C. serrulatus*) exhibiting heterozygosity for at least one translocation. Numerous plants were heterozygous for more than one translocation, and the mean number per plant was 1.3. *Calylophus serrulatus* is a complex structural heterozygote and all individuals observed were heterozygous for at least five or six translocations. Hybridization experiments with *C. berlandieri* suggested that *C. serrulatus* maintains structural hybridity with gametophytic lethals in pollen and embryo sacs.

The basic chromosome number of the genus is $x = 7$. Tetraploidy was observed in individuals from 5 of 62 populations of *C. hartwegii* that were examined. A few plants of several taxa possessed diminutive chromosomes ranging from 1 to 11 in number. The most frequent observation was of a single dark-staining pair in addition to the normal complement.

Chromosome observations of hybrids showed profound intersectional differences in structure, primarily from translocations. Translocation differences are also marked among populations in sect. *Calylophus*, but are slight among the taxa of sect. *Salpingia*.

The breeding systems of *Calylophus* are varied, with *C. serrulatus* self-compatible and highly autogamous and the other species self-sterile. *Calylophus berlandieri* and *C. tubicula* have short floral tubes, strong ultraviolet contrast patterns, matinal anthesis, and are visited by a variety of diurnal insects. Anthesis of the remaining members of sect. *Salpingia* occurs in the afternoon or evening. These plants possess long floral tubes, variable ultraviolet contrast patterns, and are visited by sphingid moths and crepuscular bees in numbers that vary from locality to locality.

Biosystematic studies of the genus *Calylophus* were begun in 1967, shortly after it had become apparent that this genus constituted a natural group no less distinct from *Oenothera* than from other genera of the tribe Onagreae (Raven, 1964). This paper is based on those studies and on an examination of extensive

[1] This study was initiated as a doctoral dissertation at Stanford University (Towner, 1970b), and subsequently amplified. I would like to express great appreciation to Peter H. Raven, at whose suggestion this research was begun. His advice and generous assistance have been invaluable throughout the course of the study. He, D. E. Breedlove, and D. P. Gregory provided both material of *Calylophus* and unpublished information on pollination. Sharon Stewart gave me indispensable assistance in the field, laboratory, and greenhouse. Dan Holmes and Judith Lynch assisted me in the field. Steven and Ann Seavey were most helpful in the maintenance of cultivated plants and the handling of herbarium material. John H. Thomas directed the processing of herbarium loans. The illustrations of flowers were drawn by Julie Spranza.

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herbarium material. A preliminary publication stemming from this research (Towner & Raven, 1970) was based on a less complete study of herbarium material and some of the taxonomic decisions made then are changed in the present paper.

The genus *Calylophus* is distinguished from the other genera of the Onagreae by the following suite of characteristics: a peltate stigma which may be discoid or nearly square in shape, sometimes with 4 shallow, broad lobes; microsporogenous tissue divided into packets in the locules of the anthers; yellow flowers; and a many-seeded capsule. In the opinion of Raven (1964), *Calylophus* is most closely related to those genera of the Onagreae which share the feature of divided microsporogenous tissue: i.e., *Gaura*, *Clarkia*, *Heterogaura*, and perhaps *Hauya*. The genus occurs over much of the Great Plains, extending into the mountains of the Great Basin region and other parts of the Southwest, and also reaching southward to the Mexican Plateau. The area of greatest diversity for the genus includes West Texas, southern New Mexico, and north-central Mexico. Populations are usually colonial and widely scattered, often occurring in disturbed areas. Habitats occupied by the species of *Calylophus* are typically somewhat xeric plains or hills with soil that is often calcareous. Plant associations in which the various forms occur range from creosote bush scrub in the Chihuahuan Desert to pine forests of several types.

The history of the genus *Calylophus* has involved several transfers at the generic level as various authors have seen fit to separate the group from *Oenothera* or to unite the two genera. Traditional treatments of the species here considered have placed them in *Oenothera* subgenera *Salpingia* and *Calylophus* or in the respective genera *Galpinsia* and *Meriolix*. Rafinesque (1819) was the first to distinguish a species of what is now *Calylophus* from *Oenothera*, although his publication, lacking a description of the genus, was invalid. The name *Meriolix* was validated only later, by Endlicher, in 1840. *Calylophus*, the first generic name of legitimate publication, was presented by Spach (1835a) and emended by him to "*Calylophis*" without justification in the same year (Spach, 1835b). It thus has priority over *Meriolix*, *Galpinsia*, and *Salpingia* at the generic level. Most of the nineteenth century treatments of the species of *Calylophus* retained them in *Oenothera*. In the late nineteenth century and until quite recently, the generic names *Meriolix* and *Galpinsia* were frequently used for the various species of *Calylophus* in treatments such as those of Heller, Small, and Rydberg.

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During the nineteenth century the explorations and collecting of Nuttall, Wright, Lindheimer, Berlandier, Hartweg, Fendler, James, Cockerell, and Toumey provided type material for most of the presently known taxa in the genus. All taxa now considered valid, except *Calylophus hartwegii* subsp. *maccartii* and *C. tubicula* subsp. *strigulosus*, were described and published between 1817 and 1898. Over this period and during the early twentieth century a number of names were proposed for minor variants, especially by Léveillé, Small, and Nelson. These contributed additional confusion to the taxonomy of the genus, which in any circumstance would have been difficult to interpret. The situation was greatly improved with the publication of Munz's (1929) revision of these species, a treatment which brought together the information available at that time and gave relative order to the taxonomy of the group. Many superfluous names were reduced to synonymy and for the first time decisions were based on adequate herbarium material. Some of the species boundaries remained unclear even then because of the complexity of variation in sect. *Salpingia*, an erroneous appraisal of the type of *C. hartwegii*, and the absence of information on breeding systems in the *C. serrulatus* group.

Raven's (1964) paper, which brought this group of species together as the genus *Calylophus*, was closely followed by the publication of Shinners (1964). Shinners presented a taxonomy similar to that used here, except that the facts concerning breeding systems in *C. serrulatus* were not yet known, and that some differences in the ranking of taxa exist between our treatments. Other differences include my recognition of *C. hartwegii* subsp. *fendleri* and a revised interpretation of *C. hartwegii* subspp. *hartwegii* and *filifolius*. In 1965 Munz published a monograph of the North American Onagraceae (Munz, 1965) in which the species of *Calylophus* were referred back to *Oenothera* and in which specific status was granted without justification to several of the entities presented by Munz as subspecies in 1929. Otherwise the taxonomy remained the same as in the earlier publication.

A brief taxonomic treatment of this group by Towner & Raven (1970), the basis of my account for the *Manual of the Vascular Plants of Texas* (Towner, 1970a), considered the species as belonging to *Calylophus*. The present work generally retains the same boundaries between taxa used in that paper. Exceptions include two changes in rank, the recognition of *C. tubicula* subsp. *strigulosus*, the reduction of *C. australis* to synonymy with *C. serrulatus*, and the changes in the names for the outcrossing members of sect. *Calylophus*. All of the foregoing changes were found necessary after a more thorough study of herbarium material was completed. *Calylophus lavandulifolius* and *C. toumeyi* were determined to be well differentiated from *C. hartwegii* and thus deserving of specific rank. *Calylophus serrulatus* is here judged to be possibly of multiple origins, and the series of populations once referred to as *C. australis* is now thought to be distinguished from other such series only by its geographical separation from the range of the rest of the species. Lastly, *C. berlandieri* was found to be the appropriate name for the entity treated by Towner and Raven as *C. drummondianus*. Type material of Drummond's was determined by an examination of pollen fertility to belong with the complex structural heterozygote *C. serrulatus*.

Cytology

Meiotic chromosome configurations were determined to establish the frequencies of structural and numerical changes in natural populations of *Calylophus*. Further, the cytology of experimental hybrids was observed in order to describe chromosomal differentiation among taxa in the genus. Previous reports of cytology in *Calylophus* (as species of *Oenothera*) include those of Hagen (1950), Lewis et al. (1958), Gregory & Klein (1960), and Kurabayashi et al. (1962). These authors reported translocation heterozygosity, tetraploidy, and extra chromosomes. P. H. Raven (personal communication) later established the presence of complex structural heterozygosity in the genus. Those phenomena were confirmed and their taxonomic distribution described in the present study. Inversion differences among populations were also found. Table 1 and the systematic accounts of the various taxa combine my findings and the results of earlier investigations.

Translocation heterozygosity is extremely common in the genus and was found in all taxa. *Calylophus serrulatus*, with its system of complex structural heterozygosity, consistently forms rings of 12 or 14 chromosomes at meiotic metaphase I. All other species form mutivalent associations regularly. Excepting tetraploids and *C. serrulatus*, 130 of 183 plants (71%) had visible translocations, and in this sample the mean number per plant was 1.3. The most frequent number of translocations per plant was 1, but individuals with 2 or 3 were common. In one observation from *C. hartwegii* subsp. *filifolius* and two from *C. berlandieri* subsp. *berlandieri*, plants were heterozygous for 5 translocations. Directed alternate disjunction seems to prevail since translocation heterozygosity does not appreciably lower pollen fertility in natural populations. Heterozygosity may well be maintained in populations by the action of heterosis, deleterious recessive genes, or even balanced lethals, especially in taxa such as *C. berlandieri* where translocation heterozygotes comprised 85% of all plants examined. In its high frequency of naturally-occurring translocations, *Calylophus* resembles some species of *Gaura* (Raven & Gregory, 1972b), *Clarkia amoena* (Lehm.) Nels. & Macbr. subsp. *amoena* (Håkansson, 1942), and some populations of *Clarkia unguiculata* Lindl. (Lewis, 1953) among the Onagraceae.

Tetraploidy was observed sporadically in some subspecies of *Calylophus hartwegii*, but nowhere else in the genus. Seven populations of *C. hartwegii* subspp. *hartwegii*, *pubescens*, *maccartii* and intermediates among them were tetraploid ($n = 14$). These plants all showed a combination of bivalents and multivalents in meiosis. No taxon was found to be wholly tetraploid, and any evolutionary significance is probably minor. Tetraploid individuals appear to arise within populations from time to time.

Extra, diminutive chromosomes were found in several taxa from both sections of *Calylophus*, and could well occur in all of the taxa. They are small dark-staining bodies that often appear to be heteropycnotic and tend to proceed through first meiotic prophase and metaphase more rapidly than the normal chromosomes. Pairing between diminutives was common, and possible associations with the larger chromosomes were seen occasionally. The most frequent observation consisted of a single diminutive pair in addition to the normal comple-

TABLE 1. Cytology of natural populations of *Calylophus*[a]

Locality	Collection	Observations
	C. berlandieri subsp. *berlandieri* (22 populations)	
New Mexico		
De Baca Co.	*130*	7_{II} (2 plants); 4_{II} + 1 ring of 6; 2_{II} + 1 ring of 4 + 1 ring of 6
Eddy Co.	*Munz & Gregory 23359*	3_{II} + 1 ring of 8 (G)
	21	7_{II}; 5_{II} + 1 ring of 4; 2_{II} + 1 ring of 4 + 1 ring of 6 + 2 dimins.
Oklahoma		
Harmon Co.	*87*	4_{II} + 1 ring of 6
Jackson Co.	*138*	$n = 7$ (5_{II} + ?)
Tillman Co.	*140*	4_{II} + 2 rings of 4; 1_{II} + 1 ring of 4 + 1 ring of 8 + 1 to 2 supernumeraries
Texas		
Brooks Co.	*60*	probable 7_{II}
	61	4_{II} + 1 chain of 6 + 2 dimins.
Calhoun Co.	*177*	3_{II} + 2 rings of 4 + 2 dimins.; 2 rings of 4 + 1 ring of 6
	179	5_{II} + 1 ring of 4; 2_{II} + 1 ring of 4 + 1 ring of 6
Garza Co.	*Raven & Gregory 19304*	4_{II} + 2_{I} + 1 ring of 4
Hartley Co.	*Roberts 35*	1_{II} + 1 ? ring of 4 + 1 ? ring of 8
Hemphill Co.	*Delso 122*	2_{II} + 1 ring of 4 + 1 ring of 6
Kenedy Co.	*186*	3_{II} + 2 rings of 4
	192	7_{II} + 1 dimin.; 5_{II} + 1 ring of 4 + 1 dimin.
Lipscomb Co.	*Rowell 10414*	7_{II}; 5_{II} + 1 ring of 4 (3 plants)
Ochiltree Co.	*158*	3_{II} + 2 rings of 4; 1_{II} + 1 ? ring of 12
Potter Co.	*91*	5_{II} + 1 ring of 4; 3_{II} + 2 rings of 4
Victoria Co.	*Bohart & Thorp 650928-1*	5_{II} + 1 ring of 4; 1_{II} + 1 ring of 4 + 1 ring of 8; 1_{II} + 2 rings of 6 + 2 dimins.
Willacy Co.	*190*	4_{II} + 1 ring of 6
	191	1_{II} + 1 ? ring of 12
Wilson Co.	*Munz & Gregory 23443*	5_{II} + 1 ring of 4 (G); $2n = 14 + 2$ extra (K); $2n = 14 + 4$ extra (K)
	C. berlandieri subsp. *pinifolius* (23 populations)	
Oklahoma		
Custer Co.	*154*	3_{II} + 2 rings of 4; 4_{II} + 1 ring of 6
Lincoln Co.	*149*	1_{II} + ? ring of 12

TABLE 1. (continued)

Locality	Collection	Observations
Logan Co.	*Raven & Gregory 19462*	5_{II} + ? ring of 4
	151	5_{II} + ? ring of 4; 3_{II} + 2 rings of 4
	152	3_{II} + 2 rings of 4
Texas		
no locality	*M. V. Brown*	7_{II} (L & B)
Bastrop Co.	*H. & M. Lewis 1636*	4_{II} + 1 ring of 6 (L)
Baxar Co.	*Klein 1671*	7_{II} (R)
	Klein 1672	5_{II} + 1 ring of 4 (R)
	Klein 1674	3_{II} + 2 rings of 4 (R)
Blanco Co.	*66*	1_{II} + 3 rings of 4
	67	5_{II} + 1 ring of 4
Brown Co.	*72*	3_{II} + 2 rings of 4
Erath Co.	*T. & L. Mosquin 5490*	5_{II}+ 1 ring of 4 (R)
Gillespie Co.	*Klein 1667*	5_{II} + 1 ring of 4 (R)
Hays Co.	*Emory*, no number (greenhouse voucher 67181)	3_{II} + 1 ? ring of 8
	Raven & Gregory 19368	4_{II} + 1 ring of 6; 3_{II} + 1 ring of 8
	Gregory 419	5_{II} + 1_{I} + 1 ring of 3 (or 4_{II} + 1_{I} + 1 ring of 5)
Kendall Co.	*Klein 1668*	7_{II} (R)
McCulloch Co.	*Munz & Gregory 23431*	2_{II} + 1 ring of 4 + 1 ring of 6 (G)
Menard Co.	*Raven & Gregory 19273*	7_{II}; 5_{II} + 1 ring of 4 (3 plants); 5_{II} + 1 ring of 4 + 1 to 2 dimins.
Mills Co.	*71*	4_{II} + 1 ring of 6
Wilbarger Co.	*77*	4_{II} + 1 ? $_{II}$ + 1 ? ring of 4
	C. hartwegii subsp. *fendleri* (15 populations)	
Arizona		
Apache Co.	*112*	5_{II} + 1 ring of 4 + 2 to 4 dimins.; 3_{II} + 1 ring of 4 + 1 chain of 4
New Mexico		
Chaves Co.	*Munz & Gregory 23346*[b]	5_{II} + 1 ring of 4 (G)
Grant Co.	*244*	3_{II} + 2 rings of 4
Otero Co.	*253*	5_{II} + 1 ring of 4; 3_{II} + 2 rings of 4
Sorocco Co.	*119*	5_{II} + 1 ring of 4
Torrance Co.	*121*	5_{II} + 1 ring of 4

TABLE 1. (continued)

Locality	Collection	Observations
	123	5_{II} + 1 ring of 4; 3_{II} + 2 rings of 4
Oklahoma		
Greer Co.	*79*	4_{II} + 1 ring of 6; 5_{II} + ?
	81	7_{II}
	85	5_{II} + 1 ring of 4 + 4 dimins.
	86	7_{II}; 5_{II} + 1 ring of 4
Texas		
Presidio Co.	*Parnell 68-T-30*	7_{II}
	R. C. Jackson in 1964	7_{II}; 5_{II} + 1 ring of 4
	26	5_{II} + 1 ring of 4; 5_{II} + 1 ring of 4 + 4 to 5 dimins.
	27	7_{II} (3 plants)
	C. hartwegii subsp. *filifolius* (8 populations)	
New Mexico		
Chaves Co.	*128*	$n = 7$
Eddy Co.	*Munz & Gregory 23357*	2_{II} + 1 ring of 4 + 1 ring of 6 (G)
	19	3_{II} + 2 rings of 4
	22	5_{II} + 1 ring of 4
Otero Co.	*Munz & Gregory 23335*	3_{II} + 2 rings of 4 (G); 7_{II}
	194	5_{II} + 1 ring of 4
Texas		
Ward Co.	*Raven & Gregory 19159*	3_{II} + 2 rings of 4
Winkler Co.	*Irving 69*	7_{II} + 1 to 2 dimins.; 1_{II} + 1 ring of 12 + 1 dimin.; 5_{II} + 1 ring of 4 + 9 dimins.; 3_{II} + 2 rings of 4 + 7 to 11 dimins.
	C. hartwegii subsp. *hartwegii* (11 populations)	
Mexico		
Aguascalientes	*McVaugh 16680*	$n = 14$, e.g., $4_{II} + 2_{IV} + 2_{VI}$
Chihuahua	*Breedlove 14305*	7_{II}
	249	7_{II} + 2 dimins.; 5_{II} + 1 ring of 4
	250	7_{II}
	252	7_{II} + 4 dimins.; 5_{II} + 1 ring of 4
Durango	*Breedlove 5947*	7_{II}; 5_{II} + 1 ring of 4
	Breedlove 14305A	7_{II} (3 plants); 5_{II} + 1 ring of 4 + 1 dimin.; 5_{II} + 1 ring of 4 + 2 dimins.

TABLE 1. (continued)

Locality	Collection	Observations
	Wiens 3464	7_{II} (R)
Zacatecas	*Breedlove 14338*	$n = 14$
	Breedlove 14344	7_{II}; 5_{II} + 1 ring of 4
	Breedlove 15485	5_{II} + 1 ring of 4
	C. hartwegii subsp. *maccartii* (10 populations)	
Mexico		
Coahuila	*53*	7_{II}; 7_{II} + 1 dimin.; 5_{II} + 1 ring of 4 (2 plants)
Nuevo León	*Waterfall 13215*	$n = 14$, e.g., $5_{II} + 3_{IV} + 1_{VI}$
	36, 38	7_{II}; 5_{II} + 1 ring of 4
Tamaulipas	*35*	7_{II}
Texas		
Kinney Co.	*Strother 299*	7_{II}; 7_{II} + 1 dimin.; 5_{II} + 1 ring of 4 (2 plants)
Maverick Co.	*34*	5_{II} + 1 ring of 4
San Patricio Co.	*Raven & Gregory 19386*	3_{II} + 2 rings of 4 (2 plants)
Val Verde Co.	*32*	7_{II}
	33	7_{II}
Zapata Co.	*Perez 42*	$n = 14$, e.g., $10_{II} + 2_{IV}$
	C. hartwegii subsp. *pubescens* (18 populations)	
Arizona		
Cochise Co.	*5, 7*	$n = 7$; 3_{II} + 2 rings of 4
	161	5_{II} + 1 ring of 4
Santa Cruz Co.	*105*	3_{II} + 2 rings of 4
New Mexico		
Chaves Co.	*12*	7_{II}
	13	7_{II}
Quay Co.	*94*	7_{II}
Oklahoma		
Custer Co.	*Munz & Gregory 23508*	$n = 7$ (K)
Greer Co.	*82*	5_{II} + ? ring of 4; 2_{II} + 1 ring of 4 + 1 ring of 6
Texas		
Brewster Co.	*Munz & Gregory 23395*	2_{II} + 1 ring of 4 + 1 ring of 6 (G)
Coleman Co.	*75*	$n = 7$
Concho Co.	*Munz & Gregory 23425*	5_{II} + 1 ring of 4 (G)

TABLE 1. (continued)

Locality	Collection	Observations
Culberson Co.	*Munz & Gregory 23364*	4_{II} + 1 chain of 6 (G)
Irion Co.	*Raven & Gregory 19211*	5_{II} + 1 ring of 4; 3_{II} + 2 rings of 4
Pecos Co.	*Munz & Gregory 23405*	$n = 14$, e.g., $3_{II} + 2_{IV} + 1_{VI} + 1_{VIII}$
Potter Co.	*92*	5_{II} + 1 ring of 4
Terrell Co.	*T. & L. Mosquin 5638*	7_{II} (R)
	Gregory 275	7_{II}; 5_{II} + 1 ring of 4; 3_{II} + 1 ring of 8
Wheeler Co.	*88*	5_{II} + 1 ring of 4
	Miscellaneous *C. hartwegii* (6 populations)	
Arizona		
Pinal Co.	*Lewis 1079* (betw. *hart.* and *pub.*)	$n = 7$ (L)
	3 (betw. *hart.* and *pub.*)	5_{II} + 1 ring of 4; $2n = 19$ to 22
New Mexico		
Guadalupe Co.	*Munz & Gregory 23516* (betw. *pubesc.* & *filif.*)	5_{II} + 1 ring of 4 (G)
Mexico		
Coahuila	*39* (betw. *macc.* & *filif.*)	$n = 14$, e.g., 10_{II} + 1 ? $_{VIII}$
Texas		
Brewster Co.	*Munz & Gregory 23401* (betw. *hart.* and *pub.*)	$n = 14$ (K)
Uvalde Co.	*Munz*, no number (no voucher seen)	7_{II} (H)
	C. lavandulifolius (7 populations)	
Arizona		
Coconino Co.	*114*	$n = 7$
Navajo Co.	*115*	7_{II} + 2 dimins.
Colorado		
Dolores Co.	*Anderson 3138*	5_{II} + 1 ring of 4
Texas		
Brewster Co.	*29*	7_{II}; 5_{II} + 1 ring of 4 (2 plants)

TABLE 1. (continued)

Locality	Collection	Observations
Nevada		
Clark Co.	*101*	7_{II}; 2_{II} + 1 ring of 4 + 1 ring of 6
	104	5_{II} + 1 ring of 4 + 4 dimins.
White Pine Co.	*Anderson 2897*	3_{II} + 2 ? rings of 4; 2_{II} + 1 ring of 4 + ? ring of 6 + 2 dimins.
	C. serrulatus (30 populations)	
No locality	***Bandar***	ring of 14 (R)
Canada		
Manitoba	***Marshall 65-1***	probable ring of 14
	Marshall 65-3	probable ring of 14
Kansas		
Ford Co.	*159*	probable ring of 14
Riley Co.	*Raven & Gregory 19483*	probable ring of 14
	Anderson 2416	probable ring of 14
Scott Co.	*160*	probable ring of 14 (2 plants)
New Mexico		
Chaves Co.	*134*	ring of 14 (2 plants)
De Baca Co.	*131*	1_{II} + probable chain of 12
Roosevelt Co.	*132*	ring of 14 (2 plants)
	133	ring of 14
Oklahoma		
Blaine Co.	*153*	ring of 14
Greer Co.	*80*	probable ring of 14
	83	probable ring of 14
Lincoln Co.	*147*	probable ring of 14
	148	probable ring of 14
Logan Co.	*150*	probable ring of 14; 1_{II} + probable ring of 12
Murray Co.	*145*	probable ring of 14
	146	ring of 14
Roger Mills Co.	*155*	probable ring of 14
South Dakota		
Lawrence Co.	*Mosquin & Mulligan 5160*	ring of 14 (R)
Texas		
Aransas Co.	*Raven & Gregory 19393*	chain of 14; probable ring of 14
	182	probable ring of 14; 1_{II} + probable ring of 12

TABLE 1. (continued)

Locality	Collection	Observations
Cameron Co.	*187*	ring of 14
	188	probable ring of 14; 1_{II} + probable ring of 12
Cochran Co.	*136*	probable ring of 14
Jackson Co.	*175*	1_{II} + ring of 12 + 2 dimins.
Matagorda Co.	*174*	possible ring of 14
San Patricio Co.	*184*	ring of 14 (2 plants); chain of 14
Wyoming		
Niobrara Co.	*Mosquin & Mulligan 5142*	ring of 14 (R)
	C. toumeyi (2 populations)	
Arizona		
Cochise Co.	*106*	3_{II} + 2 rings of 4
	107	3_{II} + 2 rings of 4; 4_{II} + 1 ring of 6
	C. tubicula subsp. *strigulosus* (1 population)	
Mexico		
Nuevo León	*U. of Kansas Exped. 119*	3_{II} + 2 rings of 4 (2 plants)
	C. tubicula subsp. *tubicula* (9 populations)	
New Mexico		
Eddy Co.	*Munz & Gregory 23350, 23353*	5_{II} + 1 ring of 4 (2 plants; G)
	14	7_{II}
	15	5_{II} + 1 ring of 4
	16	$n = 7$
	17	5_{II} + 1 ring of 4
	18	5_{II} + 1 ring of 4
Texas		
Brewster Co.	*Anderson 3030*	5_{II} + 1 ring of 4
Presidio Co.	*Munz & Gregory 23389*	7_{II} (G)
Upton Co.	*Raven & Gregory 19240*	7_{II} (4 plants)

[a] All collection numbers and chromosomal determinations are my own unless annotated as follows: (G) = Gregory & Klein, 1960; (R) = Raven, unpublished; (K) = Kurabayashi et al., 1962; (L) = Lewis et al., 1958; (H) = Hagen, 1950; (L & B) = Linder & Brun, 1957.
[b] No voucher specimen seen; identity uncertain.

ment. Numbers of extra, diminutive chromosomes ranged from 1 to 11, but the numbers were highly variable within populations and seemed to vary even among separate determinations from a single plant. The extra, diminutive chromosomes of *Calylophus* differed from those reported in *Gaura* (Gregory & Klein, 1960) and in *Oenothera* (Cleland, 1951, 1967; Cleland & Hyde, 1963) in often being heteropycnotic; pairing of the diminutive, extra chromosomes was frequent in all three genera of Onagraceae. The extra, diminutive chromosomes reported by Östergren (1947) in *Anthoxanthum* were heteropycnotic like those in *Calylophus*. Cleland (1951, 1967; Cleland & Hyde, 1963) has hypothesized that the extra, diminutive chromosomes in *Oenothera hookeri* Torr. & A. Gray, may have been derived following hybridization between this species of *Oenothera* and an entity belonging to another group of the genus. This appears doubtful since it has not been demonstrated that the chromosomes of the different groups of *Oenothera* differ significantly in size, or that their differences are or would be maintained in hybrids. Certainly, it would be very difficult to construct an analogous hypothesis for similar chromosomes in *Calylophus* and *Gaura*.

In *Calylophus*, supernumerary chromosomes of normal morphology were found only in one population of *C. berlandieri* subsp. *berlandieri* (*Towner 140*), in which plants had one to two extra chromosomes. These resembled supernumeraries as found in *Clarkia* (Lewis 1951; Håkansson, 1949), *Camissonia* (Raven, 1962), *Gaura* (Gregory & Klein, 1960; Raven & Gregory, 1972b), and *Gayophytum* (Lewis et al., 1958).

Inversion differences were encountered only in some experimental hybrids between *C. berlandieri* subspp. *berlandieri* and *pinifolius*, and also in some crosses between *C. hartwegii* and *C. lavandulifolius*. No evidence of inversion heterozygosity in natural populations was obtained, but it could well occur as an infrequent event.

Chromosomal determinations from experimental hybrids indicated that the taxa within sect. *Salpingia* have become differentiated by no more than 3 reciprocal translocations and, rarely, by an inversion. Among *C. tubicula* and all subspecies of *C. hartwegii*, crosses showed either complete homology or 1 to 2 translocation differences. *Calylophus lavandulifolius* differed from the above by 2 to 3 translocations and an inversion. The two subspecies of *C. berlandieri*, on the other hand, have become strongly differentiated, based on the current evidence. Hybrids between them were heterozygous for 2–6 translocations and sometimes for 1 inversion. Moreover, geographically separated populations of *C. berlandieri* subsp. *berlandieri* showed differences of the same magnitude. Reciprocal crosses of *C. serrulatus* and *C. berlandieri* produced hybrids with 3–6 translocation differences. Lastly, the few determinations from intersectional hybrids between *C. tubicula* and *C. berlandieri* demonstrated differences of at least 5 translocations. In the hybrid plants meiotic chromosome pairing was variable and poor, while anaphase movement was irregular. The high degree of sterility seen in these and other intersectional hybrids was probably derived from such chromosomal causes. In contrast, hybrid pollen fertility was moderate to high for most intrasectional crosses. Lower hybrid fertility in certain intra-

TABLE 2. *Calylophus* populations examined for self-incompatibility.[a]

Taxon	Locality	Collection	Results
C. hartwegii subsp. *hartwegii*	Chihuahua, Mexico	*Breedlove 14305*	SI
	Zacatecas, Mexico	*Breedlove 14344*	SI
	Zacatecas, Mexico	*Breedlove 15485*	SI
	Durango, Mexico	*Breedlove 14305A*	SI
	Aguascalientes, Mexico	*McVaugh 16680*	SI
C. hartwegii subsp. *maccartii*	Kinney Co., Texas	*Strother 299*	SI
	San Patricio Co., Texas	*Raven & Gregory 19386*	SI
	Zapata Co., Texas	*Perez 42*	SI
C. hartwegii subsp. *filifolius*	Otero Co., New Mexico	*Munz & Gregory 23335*	SI
	Ward Co., Texas	*Raven & Gregory 19159*	SI
	Winkler Co., Texas	*Irving 69*	SI
C. hartwegii subsp. *fendleri*	Apache Co., Arizona	*Towner 112*	SI
	Presidio Co., Texas	*Jackson in 1964*	SI
C. hartwegii subsp. *pubescens*	Irion Co., Texas	*Raven & Gregory 19211*	SI
	Pecos Co., Texas	*Munz & Gregory 23405*	SI
	Terrell Co., Texas	*Gregory 275*	SI
C. lavandulifolius	White Pine Co., Nevada	*Anderson 2897*	SI
C. toumeyi	Cochise Co., Arizona	*Towner 107*	SI
C. tubicula subsp. *tubicula*	Brewster Co., Texas	*Anderson 3030*	SI
	Upton Co., Texas	*Raven & Gregory 19240*	SI
C. tubicula subsp. *strigulosus*	Nuevo León, Mexico	*U. of Kansas Exped. 119*	SI
C. berlandieri subsp. *berlandieri*	Hartley Co., Texas	*Roberts 35*	SI
	Hemphill Co., Texas	*Delso 122*	SI
	Lipscomb Co., Texas	*Rowell 10414*	SI
	Victoria Co., Texas	*Bohart & Thorp 650928-1*	SI
C. berlandieri subsp. *pinifolius*	Hays Co., Texas	*Raven & Gregory 19368*	SI
	Menard Co., Texas	*Raven & Gregory 19273*	SI
C. serrulatus	Comanche Co., Oklahoma	*Anderson 2416*	SC
	Aransas Co., Texas	*Raven & Gregory 19393*	SC
	Cameron Co., Texas	*Towner 187*	SC
	San Patricio Co., Texas	*Towner 184*	SC

[a] In most cases, tests for self-incompatibility were performed on plants grown from field-collected seed.

sectional crosses involving *C. lavandulifolius* and some involving *C. berlandieri* was correlated with cytological differences between the parental plants.

Floral Biology and Pollination

Information on floral biology is based on the field work of D. P. Gregory (1964 and personal communication) and P. H. Raven (personal communication), and on my own field work and study of cultivated plants. Collections of flower visiting insects were made, and these are to be deposited at the California Insect Survey, Berkeley. Determination of ultraviolet reflection and absorption patterns was carried out by photography with black and white film under near-ultraviolet illumination. All taxa of *Calylophus* were tested for self-incompatibility by making repeated attempts at self-pollination. Table 2 lists those populations which were tested.

The breeding systems of *Calylophus* are of three basic types. That of *C. serrulatus* is based on complex structural heterozygosity. In this species the flowers are highly autogamous, often self-pollinating before anthesis (Fig. 6). For this system insect visitation and pollen transfer are unnecessary, and are in fact uncommon in *C. serrulatus*. The other two types of systems involve self-sterility and insect pollination.

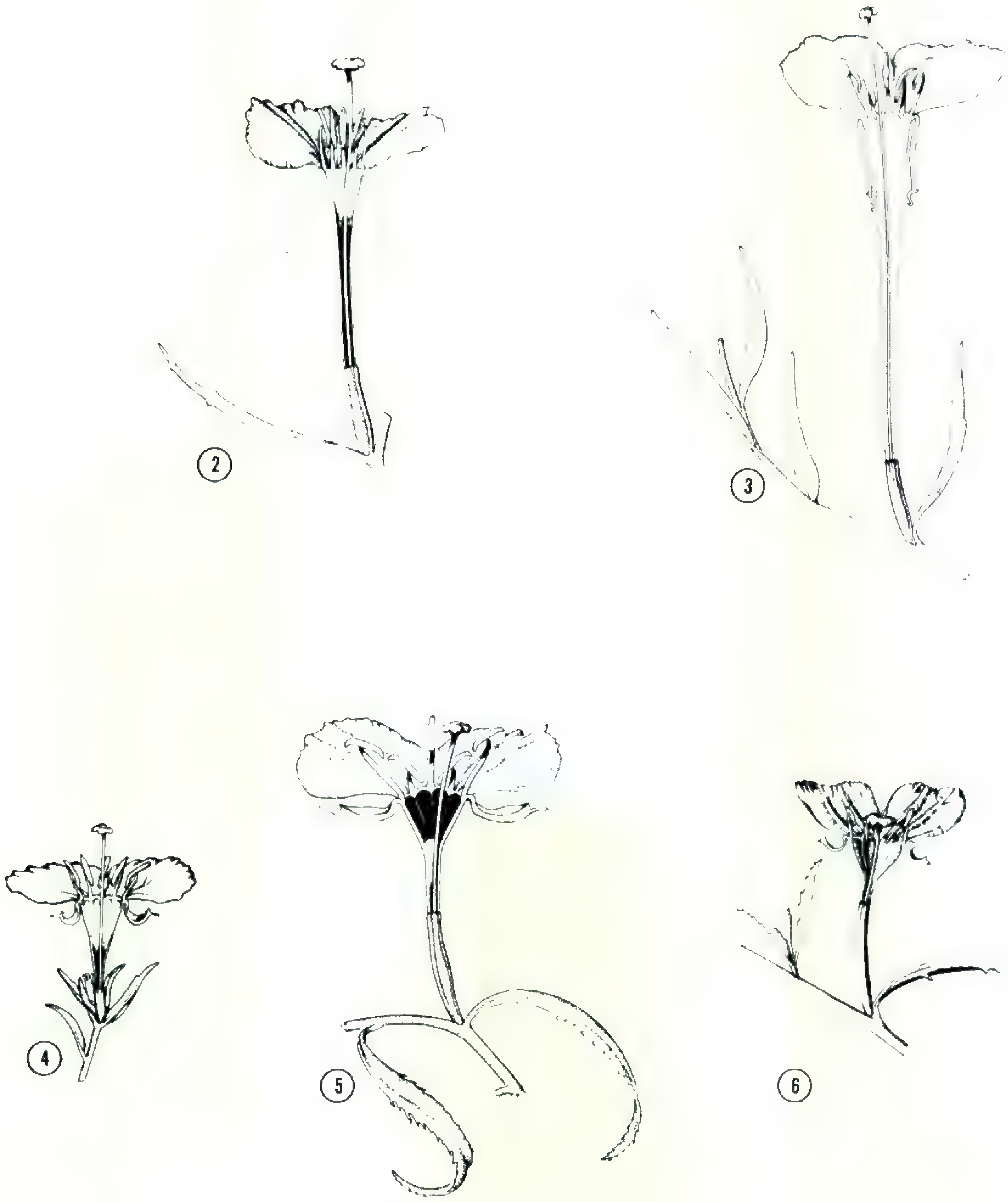
In sect. *Salpingia*, with the exception of *C. tubicula*, flowers are adapted for vespertine pollination by hawkmoths. They have narrow floral tubes measuring 25–50 mm in length (Figs. 1–3), sweet-scented nectar, large exserted stigmas, vespertine or afternoon anthesis, and, except for *C. toumeyi*, strongly ultraviolet-reflective areas on the distal portions of the petals (Figs. 7, 10). These reflective areas on the petals contrast markedly with small ultraviolet-absorptive regions which are usually present in the center of the flower. Populations of the tubular-flowered taxa experience vespertine and nocturnal visitation by hawkmoths, especially the abundant and effective pollen vector *Hyles lineata* (Fabr.) (*Celerio lineata*). Some taxa and populations within taxa of *C. hartwegii* tend to have mid-afternoon anthesis and large- to moderate-sized ultraviolet-absorptive areas in the center of the flower. These seem to be secondary adaptations for bee pollination. Many populations of taxa in sect. *Salpingia* are visited in the afternoon, early evening, and even morning by halictid, anthophorid, and other bees. Some of these are oligolectic for the Onagraceae and probably contribute to pollination. The late-opening subspecies of *C. hartwegii* (Figs. 9, 10), along with *C. lavandulifolius* and *C. toumeyi*, have ultraviolet patterns less appropriate for bee pollination. The last species has no strongly ultraviolet-reflective areas on the petals (Figs. 11, 12). In these taxa bee visitation is restricted to the early evening and is probably less effective in pollination.

Calylophus tubicula and *C. berlandieri* are pollinated by matinal and diurnal insects. Their flowers open in the early morning, have short funnelform tubes (Figs. 4, 5), and display large ultraviolet-absorptive regions in their centers (Figs. 13, 14). The petals are highly ultraviolet-reflective distally. Based on the available evidence, the primary insect visitors to *C. tubicula* seem to be morning-active halictid bees. Other potential pollinators include hawkmoths, which visit the flowers lightly at about sunrise.

FIGURE 1. *Calylophus toumeyi* in the Chiricahua Mountains, Cochise Co., Arizona (*Towner 107*).

A great variety of insects come to the flowers of *C. berlandieri*, which appears to possess a generalized pollination system. Beetles, skippers, small butterflies, occasional hawkmoths, and a wide variety of bees have been observed gathering pollen or nectar. Each of these groups may contribute to pollination, with its relative importance varying with locality.

When present, ultraviolet patterns on the flowers serve to direct insects to the anthers and nectar. The pattern typical of *Calylophus* consists of absorptive regions at the base of the petals, at the mouth of the floral tube, and on the stigma and anthers (Figs. 8, 10, 14). *Calylophus toumeyi* differs in having moderate ultraviolet absorption over the entire flower (Fig. 12). In Onagraceae, ultraviolet absorption results from the presence of one or more flavonoids with absorption maxima in the near-ultraviolet (Dement & Raven, 1973, 1974). As in many other yellow-flowered Onagraceae, the ultraviolet-absorptive portions of the petals of *Calylophus hartwegii* and *C. serrulatus*, and presumably those of the other species as well, contain isosalipurposide, a chalcone with an absorption maximum at 365 mμ (Dement & Raven, 1973, 1974, and personal communication). In addition, *C. hartwegii* has an accompanying flavonol, myrecetin-3-glucoside or galactoside, and *C. serrulatus* has an unidentified compound that resembles an aurone, a class of flavonoid that is frequently associated with chalcones in Asteraceae (W. Dement, personal communication). All of these flavonoids are absent from the ultraviolet-reflective portions of the petals. Carotenoids absorbing maximally at 400–470 mμ are found throughout the petals.



FIGURES 2–6. Longitudinal sections of flowers of *Calylophus*.—2. *C. hartwegii* subsp. *hartwegii*.—3. *C. toumeyi*.—4. *C. tubicula* subsp. *tubicula*.—5. *C. berlandieri* subsp. *pinifolius*.—6. *C serrulatus*. All × 1.1.

Therefore, insects with trichromic vision would see the petal apex color as "bee yellow" and the petal base, anthers, and stigma as "bee purple."

It is uncertain whether these ultraviolet patterns would be as effective for hawkmoth pollination after sunset as they are for diurnal insects in sunlight. The small size or absence of ultraviolet absorbing areas in the evening-opening *Calylophus* perhaps signifies that such pattens are not useful for insect orientation at night. Alternatively the minimization of ultraviolet contrast patterns may have evolved to lessen pollen and nectar removal by diurnal insects inefficient in pollinating the vespertine *Calylophus*. This could be especially true in the

FIGURES 7–12. Flowers of *Calylophus* under fluorescent and ultraviolet illumination. Collections refer to seed sources.—7. *C. hartwegii* subsp. *hartwegii* (Durango, Mexico, *Breedlove 14305A*); fluorescent illumination, emasculated.—8. Same, with ultraviolet illumination.—9. *C. hartwegii* subsp. *fendleri* (Presidio Co., Texas, *Jackson in 1964*); fluorescent illumination.—10. Same, with ultraviolet illumination.—11. *C. toumeyi* (Cochise Co., Arizona, *Towner 107*); fluorescent illumination.—12. Same, with ultraviolet illumination.

case of *C. toumeyi*, which has flowers contrasting only slightly with its vegetative parts and the background in the ultraviolet region of the spectrum. Mazokhin-Porshnyakov (1969) states that considerable ultraviolet light is present at night, especially in moonlight. However, the moths investigated have shown low sensitivities to ultraviolet light, and become functionally colorblind at light levels below 0.05 lux. Their maximum sensitivity to light is in the yellow to green

FIGURES 13–14. Flowers of *Calylophus berlandieri* subsp. *berlandieri* (Hartley Co., Texas, *Roberts* 35) under fluorescent and ultraviolet illumination.—13. Fluorescent illumination.—14. Ultraviolet illumination.

region of the spectrum. If hawkmoths follow this pattern, they could locate *Calylophus* flowers merely by their scent and reflectivity at wavelengths greater than 480 mμ, eliminating any need for ultraviolet reflection. With the moderate light levels present at dusk both bees and moths could probably utilize the ultraviolet contrast patterns for orientation.

PHYLOGENETIC RELATIONSHIPS

The species of *Calylophus* fall into two clearly recognizable but related groups. Those with keeled sepals and two sets of stamens of unequal length are included in sect. *Calylophus* and those with plane sepals and subequal stamens are assigned to sect. *Salpingia*. No intermediates between these sections have been found, and the species of the two groups are intersterile while being relatively infertile among themselves. Fifty-one of 101 intersectional crosses yielded some seed, with the amount set ranging from 5 to 81% of normal, but germination was poor (1–3%) and the few weak hybrids that grew to maturity were largely sterile (0–10% pollen fertility). Members of sect. *Salpingia* are most likely primitive in comparison with those of sect. *Calylophus*, as they have a clumped perennial habit and, except for *C. tubicula*, are primarily pollinated by hawkmoths. In growth form, the members of sect. *Salpingia* resemble the more generalized forms of *Gaura* (Raven & Gregory, 1972a), a genus which is also primarily moth-pollinated and closely related to *Calylophus*.

Among the hawkmoth-pollinated members of sect. *Salpingia*, *C. lavandulifolius* seems to be the most distinct, having a more caespitose habit than the other forms and a broad geographical distribution which includes numerous relict populations. *Calylophus toumeyi* appears to be most closely related to the southern subspecies of *C. hartwegii*, especially *C. hartwegii* subsp. *hartwegii*, with which it shares long free sepal tips, preference for montane habitats, and strigulose pubescence. Within *C. hartwegii* a pattern of reticulate relationships is evident and relative affinities are difficult to assess. *Calylophus hartwegii* subsp. *maccartii*, occupying the Texas coastal plain, is likely a recent derivative of

C. hartwegii subsp. *hartwegii*, as these two forms share several characters and are geographically adjacent. *Calylophus hartwegii* subsp. *pubescens*, *C. hartwegii* subsp. *fendleri*, and *C. hartwegii* subsp. *filifolius* seem to constitute a series of related forms occupying slightly different ecological zones in the plains of the southwestern United States. The subspecies of *C. hartwegii* are connected by zones of intergradation, although not all of the possibilities for geographical contact and gene exchange are realized. The short-lived perennial *C. tubicula* is unique in sect. *Salpingia*, having several characteristics of bee-pollinated flowers. It is likely a specialized derivative of relatively recent origin.

Sect. *Calylophus* is apparently more specialized in having an annual or short-lived perennial habit, and perhaps also in its adaptations to diurnal pollination. Of the two species in the section, *C. berlandieri* is clearly the more generalized, having a self-incompatibility system, and chromosomes which form bivalents or small rings at meiotic metaphase I. *Calylophus serrulatus*, a highly autogamous complex structural heterozygote, is a specialized offshoot of either the former species or a common ancestor. No clear knowledge of the exact ancestry of *C. serrulatus* is available, although hypothetical lineages have been worked out for some of the other complex heterozygotes in the Onagraceae. It may be that this species developed through the independent origin of complex structural heterozygosity in different geographic regions. This is suggested by the fact that neighboring populations of *C. serrulatus* and *C. berlandieri* often tend to resemble one another phenetically, a condition which could be attributable to multiple ancestry for *C. serrulatus*, to introgressive genetic exchange, or to parallel responses by the two species to local selective regimes. *Calylophus serrulatus* is highly successful and widespread in the Great Plains from Canada to New Mexico and also occurs in Arizona and Mexico. *Calylophus berlandieri* is largely restricted to Texas.

A likely but speculative evolutionary sequence could have begun with the primary divergence of the ancestors of the two sections. Accompanying this split was the development of morning anthesis and other characteristics of day-pollinated flowers in sect. *Calylophus*. The moth-pollinated perennial ancestors of sect. *Salpingia* probably evolved more slowly, but gave rise to *C. tubicula*. *Calylophus serrulatus* presumably developed very recently from *C. berlandieri* or its ancestors. The course of evolution within sect. *Salpingia* seems to have depended upon ecogeographical differentiation among the various forms, while being little dependent on cytological transformations. Cyclic climatic fluctuations in Pleistocene and Recent times have undoubtedly contributed to the taxonomic differentiation within sect. *Salpingia*, judging from the confusing patterns of overlapping geographical ranges, isolated populations, and introgression that are now in evidence among its taxa.

Divergence within sect. *Calylophus* has been marked by much greater cytological change than in sect. *Salpingia*. Several chromosomal rearrangements involving translocations were required for the derivation of *C. serrulatus* from pair-forming outcrossers. Similar chromosomal repatterning has also occurred within *C. berlandieri*, and characterizes at least three series of populations. In addition, the two races of *C. berlandieri* appear to be ecologically differentiated,

and remain well separated in regions where there exists a discontinuity between their respective habitats.

Taxonomy

Calylophus Spach, Hist. Nat. Vég. Phan. 4: 349. 1835.

"*Calylophis*" Spach, Nouv. Ann. Mus. Hist. Nat. 4: 337. 1835.
Meriolix Raf. ex Endl., Gen. Pl. 1190. June 1840; Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. 1819, nom. nud.; Raf., J. Phys. Chim. Hist. Nat. Arts 89: 259. 1819, nom. nud. TYPE: *Meriolix serrulata* (Nutt.) Walp. = *Calylophus serrulatus* (Nutt.) Raven.
Salpingia (Torr. & A. Gray) Raim. in Engler & Prantl, Natürl. Pflanzenfam. 3(7): 217. 1893. Based on *Oenothera* subg. *Salpingia* Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. TYPE: *Oenothera lavandulaefolia* Torr. & A. Gray = *Calylophus lavandulifolius* (Torr. & A. Gray) Raven.
Galpinsia Britton, Mem. Torrey Bot. Club 5: 236. 1894. Based on *Oenothera* subg. *Salpingia* Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. TYPE: *Galpinsia hartwegii* (Benth.) Britton = *Calylophus hartwegii* (Benth.) Raven.

Herbaceous to suffrutescent perennials, rarely annual, from a woody caudex, flowering in the first year. Stems nearly prostrate or decumbent to erect, with grey to pinkish brown epidermis, this sometimes exfoliating. No basal rosette, leaves cauline, more or less sessile, alternate, entire to spinuose-serrate, the upper leaves more or less uniform in size, the lowermost often somewhat larger; stipules absent. Flower 4-merous, actinomorphic, borne in the axils of the upper leaves, opening in the early morning or from midafternoon to near sunset, with the stigma receptive and anthers shedding pollen simultaneously upon anthesis or soon afterwards, wilting in 1½ to 2 days; buds erect in inflorescence. Floral tube well developed and prolonged beyond the ovary, deciduous after anthesis. Sepals greenish yellow, often with purple or red markings, reflexed separately. Petals yellow, in some species becoming red, orange, or purple upon wilting, reflexed in anthesis. Style yellow; stigma yellow to yellow green, occasionally blue black in one species, peltate, discoid to nearly square, sometimes obscurely and shallowly 4-lobed. Stamens 8, yellow; anthers narrowly elliptic to linear, versatile, the sporogenous tissue divided into packets within each locule; pollen yellow, shed singly. Capsule many seeded, sessile, cylindrical, and often narrowed at each end, obtusely 4-angled, longitudinally dehiscent, persisting on the stem after dehiscence. Seeds in 2 rows in each of the 4 locules. Basic chromosome number, $x = 7$. Five of the six species are self-incompatible.

TYPE SPECIES: *Calylophus nuttallii* Spach = *C. serrulatus* (Nutt.) Raven.

In the accounts which follow, the taxa will be grouped according to their phenetic affinities. Specimens cited were selected to represent the ranges of morphological variation and geographical occurrence. Where possible, I gave preference to recent collections and those with numbers of duplicates. My own collections are deposited in the Dudley Herbarium of Stanford University (DS) with duplicates to be distributed.

Key to Sections

a. Sepals plane, lacking a keeled midrib; stamens subequal .... Section I. *Salpingia*
aa. Sepals with conspicuously keeled midrib; stamens biseriate, the episepalous filaments about twice as long as the epipetalous filaments .... Section II. *Calylophus*

KEY TO SPECIES

Section I. *Salpingia*

a. Floral tube funnelform in the upper two-thirds or more, or less than 15 mm long; flowers opening near sunrise .... 4. *C. tubicula*

aa. Floral tube funnelform in upper half or less, 15–55 mm long; flowers opening near sunset.

  b. With conspicuous axillary fascicles of small leaves, these up to 30 mm long; subulate sepal tips 2–9(–12) mm long; capsule thin walled and dehiscent only in the distal portion; montane distribution, northwestern Mexico to southeastern Arizona .... 3. *C. toumeyi*

  bb. With or without axillary fascicles of leaves or if present, these less than 20 mm long; subulate sepal tips 0.5–6 mm long; capsule thicker walled, dehiscent along its entire length.

    c. Plants low, frequently caespitose, mostly 0.4–2 dm high; densely gray-strigulose; sepal tips short, 0.3–3 mm long .... 2. *C. lavandulifolius*

    cc. Plants not caespitose, mostly taller and more openly branched, 0.4–4 dm high; variously pubescent or glabrous; if strigulose, sepal tips 2–6 mm long .... 1. *C. hartwegii*

Section II. *Calylophus*

a. Flowers small, the petals mostly 5–12 mm long; stigma positioned near the apex of the floral tube or slightly beyond, within the circle of anthers; 30–80% of pollen grains aborted .... 6. *C. serrulatus*

aa. Flowers usually larger, the petals mostly 9–25 mm long; stigma well exserted, usually to the end of the episepalous anthers or beyond; 85–100% of pollen grains fertile .... 5. *C. berlandieri*

Section I. **Salpingia** (Torr. & A. Gray) Towner, comb. nov.

Oenothera subgen. *Salpingia* Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. *Salpingia* (Torr. & A. Gray) Raim. in Engler & Prantl, Natürl. Pflanzenfam. 3(7): 217. 1893. *Galpinsia* Britton, Mem. Torrey Bot. Club 5: 236. 1894.

Herbaceous to suffrutescent perennials 0.4–6 dm high, glabrous to glandular-pubescent, strigulose, or with spreading trichomes. Leaves 0.3–5 cm long, entire to serrulate. Inflorescence sparse to dense; buds terete. Flowers opening in afternoon, evening, or morning. Floral tube terete, tubular and gradually expanded through its entire length, or tubular proximally and funnelform distally, 5–70 mm long. Sepals plane. Petals suborbicular to rhomboidal or squarish. Stamens nearly equal in length. Capsule promptly dehiscent upon drying, usually not curved.

TYPE SPECIES: *Calylophus lavandulifolius* (Torr. & A. Gray) Raven.

1. **Calylophus hartwegii** (Benth.) Raven, Brittonia 16: 286. 1964.

Oenothera hartwegi Benth., Pl. Hartw. 5. 1839.

Herbaceous to suffrutescent perennial arising from a woody caudex; stems one to many, sparingly to densely branched above, nearly prostrate to erect, 0.4–5 dm high, strigulose, glandular-pubescent, glabrous, or with spreading hairs, more densely pubescent above. Leaves sparsely to densely distributed along the stem, sessile or indistinctly petiolate, spreading to ascending, sometimes reflexed, linear or filiform to ovate or oblanceolate, 3–50 mm long, 0.4–12 mm wide, usually not much reduced up to the stem, variously pubescent or glabrous, the tip acute

to obtuse, the base acute-attenuate to truncate-clasping, the margin entire to serrate, frequently undulate; fascicles of small leaves 1–15 mm long sometimes present in the nonfloriferous axils; lowest stem leaves sometimes wider than above, frequently obovate to spatulate, to 65 mm long. Inflorescence lax, with rarely more than one flower at a time fresh on a stem, variously pubescent or glabrous; buds terete. Floral tube terete, tubular in the lower one-half or more, gradually expanded distally, 16–50(–60) mm long, 4–20 mm wide at the throat of pressed specimens, variously pubescent or glabrous without, the inner surface glabrous distally, sometimes minutely pubescent at the base, frequently fading to pink or purple on wilting. Sepals 7–28 mm long, 2–10 mm wide, with subulate free tips 0.5–6 mm long, plane, variously pubescent or glabrous, pale yellow-green, frequently with purple spotting or marginal stripes, fading as with the floral tube. Petals suborbicular to rhomboidal, 10–35 mm long, similar in width, highly ultraviolet-reflective, with basal ultraviolet-absorptive spot of varying size, sometimes absent, frequently turning pinkish or purplish upon wilting. Stamens subequal; filaments 4–13 mm long, glabrous; anthers 5–13 mm long. Style 25–65 (–75) mm long, usually exceeding the stamens, minutely pubescent below; stigma flat to slightly revolute, squarish, 1.5–6 mm broad; ovary 4–30 mm long, 1–3 mm wide, variously pubescent or glabrous. Capsule 6–40 mm long, 2–4 mm wide, moderately thick-walled, completely dehiscent, straight or slightly curved; seeds 1–2.5 mm long, obovoid, rounded or sharply angled, truncate at the apex. Self-incompatible. Gametic chromosome numbers, $n = 7, 14$.

TYPE: MEXICO. AGUASCALIENTES: Aguascalientes, 1837, *Theodor Hartweg 10* (K, holotype; P, isotype).

Distribution: Local and colonial to abundant and widespread on rocky, sandy, gypsum, or limestone soils in arid to relatively mesic open areas, in southeastern Colorado, southwestern Kansas, western Oklahoma, Texas (except eastern part), New Mexico, southeastern and east-central Arizona, and in Mexico from Chihuahua, northern Coahuila, and northwestern Tamaulipas south to Aguascalientes. From ca. 30 to ca. 2,500 m elevation. Flowers February to October.

As treated here, *Calylophus hartwegii* includes five intergrading subspecies. The species is distributed over much of the Southwest and northern Mexico, occupying relatively dry plains and mountain regions.

Long, slender floral tubes and vespertine anthesis characterize all subspecies of *C. hartwegii*, suggesting a basic adaptation to hawkmoth pollination. Variation among the subspecies in exact time of anthesis, in ultraviolet reflection patterns, and in flower size was observed, and is likely due to modal differences in pollination systems. Principal flower visitors included halictid and anthophorid bees and hawkmoths, but with differing proportions of these insects visiting the various populations observed. The mean length of the floral tube in this species and in *C. lavandulifolius* and *C. toumeyi* is about 30–40 mm. Anthers and stigma are well exserted beyond the tube, but tend to block the entrance to it. Short-tongued hawkmoths, such as the abundant species *Hyles lineata*

(*Celerio lineata*), land on the flower and extend their heads into the tube to obtain nectar. In doing this they pick up quantities of pollen on the head and thorax and can serve as effective agents of pollination. All subspecies of *C. hartwegii* have been tested at least once for self-incompatibility. In a brief check, each of 22 plants examined was found to be self-sterile.

Of 88 diploid plants from 55 populations examined for chromosome configuration, 56 individuals from 42 populations, including some from each subspecies, showed translocation heterozygosity. The mean number of heterozygosities per plant was 1.0 for the species as a whole. Plants with as many as 5 translocation heterozygosities were found in seed obtained from natural populations, but most individuals had only 1 or 2, displaying 1 or 2 rings of 4 chromosomes or a ring of 6 at meiotic metaphase I.

Calylophus hartwegii is a predominantly diploid species, although occasional tetraploids and plants with extra chromosomes were found. Sixteen plants from nine populations, including all subspecies but *C. hartwegii* subsp. *pubescens*, had extra diminutive chromosomes. Five of the 62 populations from which chromosome number determinations have been made contained tetraploid individuals. No population was found to be comprised of both tetraploid and diploid plants, although the low number of duplicate counts from tetraploid populations leaves this possibility open. One plant intermediate between subspp. *pubescens* and *hartwegii* (*Towner* 3) appeared to be triploid, further increasing this likelihood. Tetraploids were found in *C. hartwegii* subspp. *pubescens*, *hartwegii*, and *maccartii*, all predominantly diploid taxa.

Difficulties of interpreting the variation in this species have arisen from a number of causes. The entities in sect. *Salpingia* tend to have extensive geographical ranges which overlap and interdigitate. Minor ecological differences often separate the taxa locally. The subspecies of *C. hartwegii* are distinguished morphologically from one another by a few rather slight differences such as pubescence and leaf shape. The pattern of variation within the section is reticulate, with few characters varying concordantly. Broad areas of introgression exist between certain of the taxa, while others show greater discontinuities in areas of contact. All forms retained in *C. hartwegii* are connected either directly or indirectly by intergradation. The center of the distribution of this species in western Texas and northern Mexico is characterized by an abundance of forms occurring in near proximity and by a complex display of variation.

Absence of any significant number of intermediates in the appropriate regions indicates that *C. hartwegii*, *C. lavandulifolius*, and *C. toumeyi* should be distinguished specifically. The earlier decision to combine them (Towner & Raven, 1970) was intended to emphasize the overall unity of this group, but a subsequent thorough study of herbarium material failed to bring forth evidence of intergradation among the three species.

Populations of *C. hartwegii*, as mentioned above, occasionally occur sympatrically with *C. berlandieri*, *C. serrulatus*, and *C. tubicula*. They also frequently occur mixed with *C. lavandulifolius*, and only rarely form hybrids with that species.

KEY TO SUBSPECIES

a. Ovary (and usually stems and leaf margins) with spreading trichomes; leaves (except lowest) abruptly narrowed to truncate or slightly clasping at the base; widespread .... 1e. subsp. *pubescens*

aa. Plant without spreading trichomes; leaves gradually narrowed at the base or extremely narrow throughout.

b. Plant glabrous or nearly so; flowers opening from one hour before to one hour after sunset; widespread .... 1d. subsp. *fendleri*

bb. Plant, especially on ovary and upper stems, with some form of pubescence; flowers usually opening 2–5 hours before sunset, occasionally later.

c. Ovary and stems with short glandular pubescence; leaves glabrous to glandular-pubescent, rarely sparsely strigulose, filiform to narrowly lanceolate; gypsum or limestone flats, central New Mexico to northern Mexico .... 1c. subsp. *filifolius*

cc. Ovary, stem, and leaves usually strigulose, or if glandular-pubescent, the the leaves narrowly lanceolate to lanceolate or oblanceolate.

d. Leaves mostly 4.5 to 11 times as long as wide, usually with crinkled-undulate margins; plant sparsely strigulose or occasionally minutely glandular-pubescent; low plains from southeastern Texas to northern Mexico .... 1b. subsp. *maccartii*

dd. Leaves mostly 9 to 35 times as long as wide, usually not crinkled; plant sparsely to densely strigulose; high plains and mountains from southern Trans-Pecos Texas to Aguascalientes .... 1a. subsp. *hartwegii*

1a. **Calylophus hartwegii** (Benth.) Raven subsp. **hartwegii**; Towner in Correll and Johnston, Man. Vasc. Pl. Texas 1121. 1970.—FIG. 2.

Salpingia hartwegii (Benth.) Raim. in Engler & Prantl., Natürl. Pflanzenfam. 3(7): 217. 1893. *Galpinsia hartwegii* (Benth.) Britton, Mem. Torrey Bot. Club 5: 236. 1894. *Oenothera hartwegii* Benth. var. *typica* Munz, Amer. J. Bot. 16: 706. 1929, pro parte. *Calylophus hartwegii* var. *hartwegii*; Shinners, Sida 1: 342. 1964, pro parte. *Oenothera hartwegii* var. *hartwegii*; Munz, N. Amer. Fl., ser. 2, 5: 139. 1965, pro parte.

Oenothera greggii A. Gray var. *pringlei* Munz, Amer. J. Bot. 16: 711. 1929, pro parte. *O. pringlei* (Munz) Munz, N. Amer. Fl., ser. 2, 5: 138. 1965, pro parte. TYPE: Bachimba Canyon, Chihuahua, Mexico, 27 March 1885, *C. G. Pringle 224* (GH).

Oenothera lavandulaefolia Torr. & A. Gray var. *typica* Munz sensu Munz, Amer. J. Bot. 16: 704. 1929, pro parte. *O. lavandulifolia* var. *lavandulifolia* sensu Munz, N. Amer. Fl., ser. 2, 5: 138. 1965, pro parte.

Stems several to many, sparingly branched above, decumbent to somewhat ascending, or plant tufted, 0.5–3 dm high; plant grayish-strigulose throughout, more densely so on the ovary and inflorescence than elsewhere. Leaves dense on stems, more or less ascending, linear to narrowly lanceolate, 10–35 mm long, 0.5–4 mm wide, the tip acute, the base acute-attenuate, the margin entire to shallowly and sparsely serrulate, occasionally undulate; fascicles of small leaves 2–15 mm long usually present in the axils. Floral tube (18–)30–50(–60) mm long, 4–13 mm wide at the throat, sometimes with purple longitudinal bands, often fading purplish. Sepals 8–20 mm long, 3–7 mm wide, with free tips (1–)2–6 mm long, frequently with purple marginal stripes. Petals squarish or rhomboidal, 13–30 mm long, frequently fading to a purple or pink color, with basal ultraviolet-absorptive spot absent or present and of small to moderate size. Filaments 5–10 mm long; anthers 5–9 mm long. Style 30–65(–75) mm long, glabrous; stigma 2–5 mm broad; ovary 5–12 mm long, 1–2 mm wide. Capsule 10–25 mm long, 2–4 mm wide; seeds 1–2.5 mm long. Self-incompatible. Gametic chromosome numbers, $n = 7, 14$.

FIGURE 15. Distributions of *Calylophus hartwegii* subsp. *hartwegii* (dots), *C. hartwegii* subsp. *maccartii* (triangles), and intergrades between the two subspecies (open circles).

Distribution (Fig. 15): Mostly on rocky or gravelly soil, sometimes limestone, in rugged canyons in the northern part of the range, to high plains and mountains, reaching pine forest at the southern limits of the range, from Brewster and southern Hudspeth cos., Texas, south through central Chihuahua, Coahuila, western Nuevo León, and eastern Durango to central and southeastern Zacatecas, Aguascalientes, and southwestern San Luis Potosí. Elevational distribution from ca. 900 m (near Solis, Brewster Co., Texas) to at least 2,300 m (6 mi N of Zacatecas, Zacatecas, Mexico). Flowers February to October.

Representative specimens examined:

UNITED STATES. TEXAS: Brewster Co.: Nr. Solis, just N of Mariscal Canyon, Big Bend National Park, *Johnston & Correll 24568* (LL). Head of Fresno Canyon, Big Bend Ranch, *Correll & Rollins 23672* (LL). Near Marathon, *Young 174* (MO, TEX). Hudspeth Co.: Panther Hill–Fox Hill area of the central Malone Mts., *Waterfall 5830* (GH, NY). Val Verde Co.(?): Pecos R., *Thurber 123* (NY). County unknown: Coyote Mt., West Texas, *Havard 37704* (CAN).

MEXICO. CHIHUAHUA: 12 mi W of General Trías, *Breedlove 15741* (DS). 5 mi S of Hidalgo del Parral, *Breedlove 15745* (DS). 13 mi E of Hidalgo del Parral, *Breedlove 14305* (DS). Santa Eulalia Mts., *Rose 11693* (US). Santa Eulalia Hills, *Wilkinson 4601* (F, NY). Ca. 30 mi NW of Chihuahua, *Lee 59* (F, TEX). Vicinity of Chihuahua, *Palmer 59* (F, MO, NY, US). Alberto, SE of Chihuahua, *Pennell 18627* (NY, PH, US). 11 mi N of Parral, *Waterfall 12514* (OKLA). Chihuahua, *Le Sueur 130* (F, UC). Between Parral and Villa Ocampo, *Weber & Charette 11710* (COLO). Gallego Springs (between Carrizal and Chihuahua), *Wislizenius in 1846* (MO). Near Chihuahua, *Pringle in 1886* (F, MO, NY, US). 13 mi N of Ciudad Chihuahua, *Breedlove 15736* (DS). 24 mi W and 1 S of Chihuahua, *Stuessy 1020* (TEX). 23 mi W of Chihuahua, *White 2470* (ARIZ). Near Chihuahua, *Le Sueur 811 = 58* (F, MO, SMU, TEX, US). COAHUILA: Múzquiz, Palm Canyon, *Marsh 1002* (F, OKLA, TEX). Múzquiz, *Marsh 1134* (F, OKLA, SMU, TEX). Cerro de los Árboles, *Jermy 147* (US). 11 km NE of Jimulco, *Stanford et al. 9* (ARIZ, DS, MO, NY, UC, WTU). 24 km NW of Fraile, *Stanford et al. 402* (ARIZ, DS, MO, NY, WTU). Sierra Mojada Mts., *Jones 233* (MO, POM, US). Sierra Mojada, *Jones in 1891* (POM). Near Patos (now General Cepeda), *Gregg 723* (MO). Near Buena Vista, SW of Saltillo, *Gregg 387* (MO). Ciénega Grande (just NE of Parras), *Gregg 492* (MO). Allende, *Marsh 1776* (F, TEX). Sierra de la Paíla, *Purpus 4977* (F, US). Sierra de Parras, *Purpus in 1905* (UC). Saltillo, *Arsène 6510* (US). Paso del Diamante, near Saltillo, *Munz 15034* (MO, POM). 30 mi W of Saltillo, *Wislizenius 298* (MO). Saltillo (?), *Palmer 344* (US). Saltillo, *Palmer 337* (US). 9 mi S of Saltillo, *Straw & Forman 1337* (RSA). Ca. 20 mi E of Saltillo, *McVaugh 12301* (RSA). Saltillo, *Fisher 32* (F, UC). NUEVO LEÓN: 12 mi N of Sabinas Hidalgo, *Heard & Barkley 14535* (TEX). 4 mi S of Galeana, *McGregor et al. 65* (DS, KANU, SMU). DURANGO: 46 mi N of La Zarca, *Straw & Forman 1525* (RSA). 15 km NE of Guadalupe Victoria, *Henrickson 1762* (DS). 77 mi S of Parral, *Wiens 3464* (COLO, DS). 6 mi NE of Hidalgo del Parral, *Breedlove 5947* (DS). 21 mi N of La Zarca, *Breedlove 14305A* (DS). 71 mi NE of Durango, *Waterfall 13336a* (OKLA, RSA, SMU). 3–6 mi W of La Zarca, *Straw & Forman 1717* (RSA, UC). Ca. 54 mi S of Villa Matamoros, Chihuahua, *Straw & Forman 2058* (RSA, UC). ZACATECAS: On route 49, 2 km N of Route 45, *Cruden 1238* (DS). Near Concepción del Oro, *Palmer 271* (F, MO, NY, UC, US). Gypsum flats, Sierra Hermosa, *Shreve 8594* (ARIZ). 2 mi SE of Sombreto (Sombrerete?), *Waterfall 13799* (OKLA, RSA, SMU). 7 mi S of Fresnillo, *Breedlove 15485* (DS). 9 mi N of Fresnillo, *Breedlove 15486* (DS). 2 mi SW of Sain Alto, *Breedlove 5952* (DS). 6 mi N of Zacatecas, *Breedlove 15481* (DS). 21 mi N of Sombrerete, *Breedlove 14338* (DS). 27 mi N of Fresnillo, *Breedlove 14344* (DS). Concepción del Oro, *Pennell 17416* (PH). "Gravelly soil," *Purpus in 1903* (UC). Ca. 22 mi NE of Zacatecas, *Straw & Forman 1492* (RSA). 55 mi W of Zacatecas, *Reveal et al. 2660* (DS). SAN LUIS POTOSÍ: 8 km NE of Laguna Seca, on km 20 of road from San Luis Potosí to Antiguo Morelos, *Rzedowski 6325A* (RSA). Charcas, *Whiting 898* (ARIZ). Ca. 5 km NNE of Matehuala, *Rzedowski 9186* (DS). 44 mi NW of San Luis Potosí on road from Zacatecas, *Breedlove 5954* (DS). 13 mi NW of San Luis Potosí on road to Zacatecas, *Breedlove 14346* (DS). 27 mi NW of San Luis Potosí along road to Zacatecas, *Breedlove 15473* (DS). Charcas, *Lundell 5125* (ARIZ, DS, F, POM, UC, US). AGUASCALIENTES: 9 mi E of Aguascalientes, *McVaugh 16680* (RSA, TEX). JALISCO(?): Lake Chapala (locality almost certainly in error) *Lemmon & Lemmon in 1905* (UC).

Calylophus hartwegii subsp. *hartwegii* occupies a diversity of habitats, including desert scrub, thorn scrub, and pine forest. Typical material for this subspecies comes primarily from montane areas of north-central Mexico, while collections from lower altitudes and more northern localities exhibit evidence of hybridization with other taxa. Poor sampling in the remoter areas of northern Mexico has left details of the geographical range unclear. For example, the occurrence of this subspecies throughout most of northern Coahuila and eastern Chihuahua seems likely, but is not yet established.

The limits of the variation in this subspecies do not correspond closely to those set by Munz (1929) for *Oenothera hartwegii* var. *typica.* The strigose pubescence of Hartweg's type actually excludes it from Munz's description, and the bulk of the present taxon would also not be included. *Oenothera greggii* var. *pringlei* was named to accommodate the strigose-canescent forms, but since Hartweg's original type represents that group of populations var. *pringlei* must be reduced to synonomy. On the basis of leaf width, I have placed some elements of Munz's var. *typica* in *C. hartwegii* subsp. *maccartii.* In addition, a portion of Munz's var. *typica* which included glandular-pubescent individuals is joined with *C. hartwegii* subsp. *filifolius,* as is part of Shinner's *C. hartwegii* var. *hartwegii.* Lastly, some collections with glabrous leaves and stems placed in var. *typica* by Munz and in var. *hartwegii* by Shinners clearly belong with *C. hartwegii* subsp. *fendleri* as it is here constituted. In all previous treatments, the composition of var. *hartwegii* has been extremely heterogeneous. Clear identification of the nature of Hartweg's type and the recognition of larger geographical assemblages have rendered the variation pattern for *C. hartwegii* less confusing, especially with regard to subsp. *hartwegii.* Finally, a few plants assigned to *Oenothera lavandulaefolia* by Munz clearly belong with *C. hartwegii* subsp. *hartwegii* on the basis of their long sepal tips, narrow leaves, and southern distribution.

Considerable variation in leaf width, stature, and degree of pubescence exists in this subspecies. Especially pubescent plants with small leaves occur in Chihuahua and northern Durango. High montane plants tend to be shorter and more tufted, while the stems of low altitude plants are longer and more erect. Broader leaves occur in the latter populations, especially where they intergrade with *C. hartwegii* subsp. *maccartii* in northeastern Mexico and in western Texas, an extensive zone occupied by intermediates between subspp. *hartwegii* and *pubescens.*

In one field study, D. E. Breedlove (personal communication) found anthesis in a population of this form to occur by 1 to 1¾ hours after sunset (San Luis Potosí, *Breedlove 15473*). However, no insects visited the flowers during the period of his observations. In the state of Chihuahua, Mexico I observed several bees (*Agapostemon, Apis*) and small butterflies on freshly opened flowers in the midafternoon (*Towner 247*). Anthesis in Chihuahuan populations occurred from 4½ to 2 hours before sunset. Greenhouse-cultivated plants from a wide range of Mexican localities showed great variation in opening times, extending from 4½ hours before sunset to sunset. This variation in anthesis times may be a result of latitudinal or seasonal differences in photoperiod or a product of adapta-

tion to locally differing insect faunas. Regional ecological differentiation may well have occurred within this subspecies since the southern forms from pine forests seem to open much later than those inhabiting scrub and grasslands in the plains and hills of Chihuahua. Hawkmoths are undoubtedly regular evening visitors to all populations of subsp. *hartwegii.* Ultraviolet-absorbing areas on the petals can be nearly absent, present along the basal portion of the veins, or present as a small basal spot (Fig. 8). This suggests that some populations, i.e., those with spots absent, may be exclusively moth-pollinated while those with spots and early anthesis may be visited by bees active in the late afternoon.

Chromosomal variation in this subspecies includes polyploidy, translocation heterozygosity, and extra chromosomes. Two of 11 populations, 1 from Aguascalientes and 1 from Zacatecas, yielded tetraploid counts. Translocation heterozygosity was found in 7 of 17 diploid plants examined and in 6 of 9 populations from which meiotic determinations were obtained. The mean frequency of translocations per plant, 0.4, was the lowest for any taxon in the genus. Four plants of this subspecies had 1 to 4 extra diminutive chromosomes. Examination of hybrids indicated that one population of *C. hartwegii* subsp. *hartwegii* differed from the other taxa in sect. *Salpingia* by one or two translocations.

Introgression of *C. hartwegii* subsp. *hartwegii* with other taxa appears to occur widely, especially with subspp. *pubescens* and *maccartii.* Intermediates between subspp. *pubescens* and *hartwegii* exist in southern West Texas, southeastern Arizona, and probably in northern Chihuahua and Coahuila. Regions of intermediate altitude in northeastern Mexico and along the upper Rio Grande River in southern Texas contain populations varying on a continuum between subspp. *maccartii* and *hartwegii.* As mentioned on p. 99, *C. tubicula* subsp. *strigulosus* may represent a stabilized derivative of introgression between *C. tubicula* subsp. *tubicula* and *C. hartwegii* subsp. *hartwegii.* Lastly, plants with narrow leaves, but lacking dense strigose pubescence, occur near Saltillo in southern Nuevo León and may represent introgressants with *C. hartwegii* subsp. *filifolius,* which occurs to the south of that area, or alternatively they may be independent narrow-leaved derivatives of the species.

No examples of sympatry without hybridization have been documented for *C. hartwegii* subsp. *hartwegii* and other taxa. The recent discovery of *C. lavandulifolius* in southern Nuevo León opens the possibility that it might come into contact with *C. hartwegii* subsp. *hartwegii.* Those two taxa proved somewhat intersterile in laboratory crosses, and might not be expected to hybridize extensively in the field.

1b. **Calylophus hartwegii** (Benth.) Raven subsp. **maccartii** (Shinners) Towner & Raven, Madroño 20: 243. 1970.

Calylophus hartwegii (Benth.) Raven var. *maccartii* Shinners, Sida 1: 343. 1964.
Oenothera greggii A. Gray var. *pringlei* Munz sensu Munz, Amer. J. Bot. 16: 711. 1929, pro parte. *O. pringlei* (Munz) Munz sensu Munz, N. Amer. Fl., ser. 2, 5: 138. 1965, pro parte.

Stems several to many, sparingly branched above, nearly prostrate to ascending, 0.5–5 dm high; plants glandular-pubescent or minutely strigulose. Leaves

sparse to dense on stems, spreading to more or less ascending, narrowly lanceolate to lanceolate or oblanceolate, rarely linear, 6–35 mm long, 1–6 mm wide, nearly glabrous to sparsely strigulose or glandular-pubescent, the tip acute, the base acute-attenuate, the margin subentire to serrulate, usually undulate or undulate-crinkled; axillary leaves present, to 15 mm long. Inflorescence sparsely to densely strigulose. Floral tube 17–45 mm long, 5–12 mm wide at the throat. Sepals 11–27 mm long, 2.5–7 mm wide, with free tips 1–6 mm long, occasionally with purple marginal stripes. Petals nearly orbicular to squarish, 10–30 mm long, frequently fading purple or pinkish, with a conspicuous, large basal ultraviolet-absorptive spot. Filaments 6–12 mm long; anthers 5–9 mm long. Style 25–60 mm long, glabrous above to minutely pubescent basally; stigma 2–4 mm broad; ovary 5–15 mm long, 1.5–2 mm wide. Capsule 10–22 mm long, 2–3 mm wide; seeds 1–2 mm long. Self-incompatible. Gametic chromosome numbers, $n = 7$, 14.

TYPE: UNITED STATES. TEXAS: Starr Co., U.S. Highway 83, 6 mi NW of Rio Grande, in mesquite savannah, 24 March 1963, *Rosa Ena Benavides 91* (SMU, holotype; TEX, isotype).

Distribution (Fig. 15): Common semiarid grassy flats, in sandy to gravelly soil, often of limestone, frequently with *Prosopis glandulosa*, *Opuntia*, *Acacia*, *Larrea divaricata*, and *Yucca*, on the South Texas Plains and along the Rio Grande from Val Verde, Kinney, Uvalde, and Milam cos., Texas, south to southeastern Coahuila, central Nuevo León and northwestern Tamaulipas. From elevations of ca. 30 m (4 mi NW of Mathis, San Patricio Co., Texas) to ca. 1,500 m (Saltillo, Coahuila). Flowers March to September.

Representative specimens examined:

UNITED STATES. TEXAS: Dimmit Co.: E of Carrizo Springs, *Jones 28153* (MO, POM). 8 mi S of Catarina, *McGregor 16774* (DS, KANU). Duval Co.: 10 mi SW of Benavides, *García 113* (OKLA, SMU, TEX). 16 mi NE of Freer, *Malacara & Gutiérrez 30* (LL, SMU). San Diego, *Tharp 6031* (TEX, US). 7 mi E of Freer, *Rodríguez 104* (OKLA, SMU, TEX). Goliad Co.: Goliad, *Williams 110* (PH, TEX). Jim Hogg Co.: 2 mi N of Santa Elena, *Ríos & Cavazos 68* (LL). Jim Wells Co.: 23 mi N of Alice, *Painter et al. 14436* (LL, TEX). 8 mi N of Alice, *Bruni et al. 13* (LL). 15 mi NW of Alice, *Castillo 20* (DS, SMU). Kinney Co.: Spofford, *Treleau in 1900* (MO). Ca. 20 mi NE of Brackettville, *Strother 299* (SMU, TEX). 26.0 mi SE of Del Rio, *Towner 34* (DS). La Salle Co.: Encinal, *Vásquez 43* (DS). Live Oak Co.: 11.5 mi S of George West, *Cory 28531* (POM). 8 mi S George West, *Flyr 353* (DS, SMU). Maverick Co.: 30 mi SW of Eagle Pass, *Bruni 8* (LL, OKLA, SMU, TEX). 5 mi N of Eagle Pass, *Rowell 8824* (LL, OKL, OKLA). Eagle Pass, *Schott in 1852* (F). San Patricio Co.: 4 mi NW of Mathis, *Raven & Gregory 19386* (DS). Uvalde Co.: 5 mi W of Uvalde, *Munz 15558* (POM). Sabinal, *Jones 29563* (POM). Val Verde Co.: Near Comstock city limits, *Warnock & Turner 696* (SMU). N of Del Rio, *Jones 28158* (MO, POM). Devil's River, *Earle & Earle 441* (MO, NY, US). Ca. 20 mi NNW of Del Rio, *McVaugh 8259* (DS, F, SMU, TEX). Ca. 23.5 mi NW of Del Rio, *Towner 32* (DS). 3.4 mi SE of Del Rio, *Towner 33* (DS). Webb Co.: Minera, *Reverchon 3558* (MO, US). 10 mi S of Laredo, *Cisneros 15* (LL, OKLA). Laredo, *Crockett 6444* (LL, US). 11 mi S of Laredo, *Robles 14* (SMU). 8 mi NW of Laredo, *Ramírez 45* (DS, SMU). 23 mi NW of Laredo, *McCart 7270* (OKLA). 9.5 mi S of Laredo, *Cory 28118* (POM). Zapata Co.: Zapata, *Pérez 42* (DS). Near Zapata, *Wood 42* (TEX). 5 mi S of San Ignacio, *Rodríguez 27* (SMU). 3 mi S of Zapata, *Sánchez 85* (OKLA, TEX). Zapata, *Guajardo 32* (LL, SMU). 2 mi SE of Zapata, *González-Arroyo 92* (LL, OKLA, SMU).

MEXICO. TAMAULIPAS: Along the river road, 20 mi E of the International Highway, *Escalante 55* (SMU, TEX, OKLA). 3 mi SW of Headquarters, Loreto Ranch, *Crutchfield & Johnston 5568A* (TEX). 50 mi SE of Nuevo Laredo, *García & García 35* (DS, WTU). NUEVO LEÓN: 24 mi W of Monterrey, *Waterfall & Wallis 13214, 13215* (RSA, SMU). Monterrey,

Fisher 272 (MO, US). Río Santa Catarina, Monterrey, *Arsène 6306* (MO, US). 65 mi S of Nuevo Laredo, *Frye & Frye 2369* (DS, MO, NY, RM, RSA, SMU, UC, WTU). 9 mi S of Nuevo Laredo, *Frye & Frye 2390* (NY, RSA, UC, US, WTU). 12 mi N of Sabinas Hidalgo, *Barkley & Heard 14535* (F, MO, US). 17 mi NE of Sabinas Hidalgo, *Rodríguez 70* (SMU, TEX). 16 km W of Sabinas Hidalgo, *Domínguez & McCart 8255* (SMU, TEX). 45 mi S of Nuevo Laredo, *McCart et al. 8133* (OKLA, SMU, TEX). Sabinal (?), *Jones 29563* (MO, UC). Monterrey, *Dodge 158* (US). Between Monterrey and Reynosa, along side road to San Juan, *Langman 2870* (DS, PH). Monterrey, *Edwards & Eaton in 1846* (NY). 50 mi S of Laredo, *Hess & Hall 637* (OKL). Ca. 54 mi S of the U.S. border in Laredo, *Towner 35* (DS). 39 mi N of center of Monterrey, *Towner 36* (DS). COAHUILA: 9 km S of Parras, Sierra Negra, *Stanford et al. 158* (ARIZ, MO). Near Díaz (now Piedras Negras), *Pringle 8304* (DS, F, MO, PH, POM, RM, RSA, UC, US). Ciudad de Porfirio Díaz, *Canby 109* (US). Guadalupe, *Aguirre 703* (RSA). Parras, *Aguirre & Reko 82* (NY). Ca. 48 mi N of Saltillo, *Jackson 6722* (KANU). 25 km S of Piedras Negras, *Rinehart 218* (OKL, OKLA, RSA). 13.4 mi S of central Saltillo, *Towner 52, 53* (DS).

Closely related to *Calylophus hartwegii* subsp. *hartwegii*, this subspecies occurs at higher latitudes and lower elevations. It is relatively common in disturbed areas in the grasslands of southern Texas. It corresponds closely to var. *maccartii* as treated by Shinners except that narrower-leaved plants are included here. The broad leaves, which are frequently oblanceolate, early afternoon anthesis, and sparser, often glandular pubescence serve to distinguish this subspecies from subsp. *hartwegii*. Only leaf dimensions serve adequately in separating subspp. *maccartii* and *filifolius*. Considerable phenotypic variation occurs in subsp. *maccartii* in terms of pubescence, leaf shape, stature, and nature of the leaf margin. Leaf margins may be serrulate, undulate, or subentire.

Pollination was studied near Saltillo, Coahuila, Mexico (*Towner 52, 53*) at a roadside population of *C. hartwegii* subsp. *maccartii*. Anthesis was not observed, but had been completed by 2¼ hours before sunset. Most visitors to the flowers were halictid bees, especially *Evylaeus* and *Agapostemon*, some of them possibly oligoleges. These may have played some part in pollination in the late afternoon and morning in spite of their small size. No large native bees, except for a single *Bombus*, and no hawkmoths were observed visiting flowers, but their involvement cannot be discounted on the limited evidence available.

Greenhouse studies showed anthesis times occurring 3–5 hours before sunset and flowers with large central ultraviolet-absorbing areas. Self-incompatibility was found in the 3 plants available for testing. This suggests that *C. hartwegii* subsp. *maccartii* has perhaps secondarily shifted from hawkmoth pollination, as indicated by its morphology, to bee pollination, as might be inferred from its ultraviolet pattern and behavior.

Two of 10 populations showed tetraploidy, in addition to 1 population intermediate between *Calylophus hartwegii* subspp. *filifolius* and *maccartii*. One plant from each of 2 populations had a single extra diminutive chromosome. Half of 16 plants, representing 5 of 8 diploid populations, were heterozygous for translocations. The mean frequency of translocation heterozygosities was 0.6 per plant, and only one plant had as many as 2. Experimental hybrids between *C. hartwegii* subsp. *maccartii* and other members of sect. *Salpingia* were heterozygous for 1 or 2 reciprocal translocations.

Introgression occurs, as mentioned above, with *C. hartwegii* subsp. *hartwegii* in southern Texas and northeastern Mexico. It also appears to have taken place

with subsp. *pubescens* along the upper Rio Grande in southern Texas, although there is difficulty in recognizing the sources of variation in this region. Two further collections [36 mi W of Monterrey, Coahuila, Mexico, *Towner 39* (DS). 5 mi W of Marathon, Brewster Co., Texas, *Warnock 60004* (TEX)] appear to be intermediate between subspp. *maccartii* and *filifolius*, although this may not necessarily have resulted from introgression. The only other taxon of *Calylophus* occurring near *C. hartwegii* subsp. *maccartii* is *C. berlandieri* subsp. *berlandieri*. The two are essentially intersterile, but in the South Texas Plains have often been mistaken for one another because there they tend to resemble each other in leaf shape and character of the margin.

1c. **Calylophus hartwegii** (Benth.) Raven subsp. **filifolius** (Eastw.) Towner & Raven, Madroño 20: 243. 1970.

Oenothera tubicula A. Gray var. *filifolia* Eastw., Proc. Calif. Acad. Sci., ser. 3, 1: 72. 1897. *Galpinsia filifolia* (Eastw.) Heller, Cat. N. Amer. Pl., ed. 2. 8. 1900. *Oenothera hartwegii* Benth. var. *filifolia* (Eastw.) Munz, Amer. J. Bot. 16: 707. 1929. *Calylophus hartwegii* (Benth.) Raven var. *filifolius* (Eastw.) Shinners, Sida 1: 345. 1965. *Oenothera hartwegii* var. *fendleri* (A. Gray) A. Gray subvar. *filifolia* (Eastw.) H. Lév., Monogr. Onoth. 335. 1908.

Oenothera hartwegii Benth. var. *typica* sensu Munz, Amer. J. Bot. 16: 706. 1929, pro parte. *Calylophus hartwegii* (Benth.) Raven var. *hartwegii* sensu Shinners, Sida 1: 342. 1964, pro parte. *Oenothera hartwegii* var. *hartwegii* sensu Munz, N. Amer. Fl., ser. 2, 5: 139. 1965, pro parte.

Stems several to many, moderately to densely branched above, decumbent and spreading to somewhat ascending, 0.5–4 dm high; plant minutely glandular-pubescent throughout, more densely so on the ovary and inflorescence, infrequently sparsely strigulose on the ovary and leaves. Leaves moderately well-spaced to dense on the stem, spreading to ascending, filiform to narrowly lanceolate, 3–45 mm long, 0.4–3(–4) mm wide, the tip acute, the base acute-attenuate, the margin entire to remotely serrulate, occasionally undulate; axillary leaves present, to 10(+) mm long. Floral tube 16–50 mm long, 4–14 mm wide at the throat, occasionally fading pinkish. Sepals 7–17 mm long, 3–7 mm wide, with free tips 0.5–4 mm long, frequently with purple spotting and occasionally with a purple marginal stripe. Petals suborbicular to somewhat rhomboidal, 12–23 mm long, occasionally fading pinkish, with a basal ultraviolet-absorptive spot of moderate to large size. Filaments 6–13 mm long; anthers 6–11 mm long. Style 26–60 mm long, glabrous above, glabrous or minutely pubescent basally; stigma 1.5–4 mm broad; ovary 4–13 mm long, 1–2 mm wide. Capsule 7–22 mm long, 2–3 mm wide; seeds 1.2–2 mm long. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. NEW MEXICO: White Sands, probably in Otero Co., August 1896, *T. D. A. Cockerell* (CAS).

Distribution (Fig. 16): Highly local, but often abundant, almost always on semiarid gypsum flats, dunes, or outcrops, frequently with *Larrea divaricata*, *Yucca*, or *Juniperus*, from Otero and Torrance cos., New Mexico south and east through the Trans-Pecos and southern Panhandle regions of Texas, thence northeast to Cottle Co., Texas and southward from widely scattered localities in cen-

tral Chihuahua and Coahuila. Occurring from elevations of ca. 600 m (7 mi N of Spur, Dickens Co., Texas) to cà. 1,850 m (7.2 mi SE of Willard, Torrance Co., New Mexico). Flowers May to October.

Representative specimens examined:

UNITED STATES. NEW MEXICO: Chaves Co.: 20 mi S of Roswell, *Earle & Earle 293* (MO, NY, POM, RM, UC, US). 2 mi E of Bottomless Lakes State Park Headquarters, *Hess 73* (WTU). 56.7 mi SE of Vaughn, *Towner 125* (DS). 18.7 mi N of Roswell on U.S. 285, *Towner 128* (DS). De Baca Co.: 22 mi S of Fort Sumner, *Brooks & Stephens 25763* (DS). Dona Ana Co.: Jornada Game Reserve, *Wooton*, no date (US). Eddy Co.: 3 mi NW of Texas state line on U.S. 62/180, *Raven & Gregory 19156* (DS). 6 mi SW of White's City, *Munz & Gregory 23357* (POM, UC, WTU). 11.4 mi SW of White's City, *Towner 22* (DS). Lea Co.: 55–60 mi E of Roswell, *Palmer 62* (F). Lincoln Co.: White Mts., 5,400 ft, *Wooton 181* (ARIZ, DS, GH, MO, NY, POM, RM, UNM, UC, US). 22 mi N of Carrizozo, *Brooks & Stephens 25957* (DS). Otero Co.: Round Mt., along Tularosa Creek in Sacramento Mts., *Wooton in 1899* (ARIZ, DS, NMC, NY, POM, RM, US). White Sands National Monument, *Munz & Gregory 23335* (POM). White Sands National Monument, 2 mi W of headquarters, *Towner 11* (progeny, DS). Torrance Co.: Near Willard, *Wooton 2730* (COLO, DS, RM, US). 7.2 mi SE of Willard, *Towner 122* (DS). TEXAS: Culberson Co.: 2 mi SE of U.S. 62/180 at New Mexico line, *McVaugh 8164* (DS, GH, LL, SMU, TEX). 30 mi N of Van Horn, *Waterfall 4122* (GH). Dickens Co.: 7 mi N of Spur, *Moss 19* (OKLA). Ector Co.: 1 mi E of jct. of Texas 185 and U.S. 385, *Gregory 424* (DAO, DS, RSA, UC). Gaines Co.: 15 mi E of Seminole, *Lundell & Lundell 16955* (LL). Howard Co.: Big Springs, *Tracy 8306* (F, GH, MO, NEB, NY, TEX, US). Hudspeth Co.: Gypsum quarry E of Finley, *Waterfall 5023* (GH, MO). Kent Co.: 2 mi W of Clairemont on U.S. 380, *Correll & Johnston 22107* (LL). Loving Co.: Along Salt Creek near highway 285, N of Orla, *Correll & Correll 26016* (Mixed with *C. hartwegii* subsp. *pubescens*, LL). Martin Co.: E of Stanton, *Lundell & Lundell 16916* (LL). Midland Co.: 4 mi E of Midland, *Cory 42030* (POM, TEX). Nolan Co.: Sweetwater, *Reverchon 1285* (F, MO). Ward Co.: 9.5 mi S of Monahans, *Gregory 174* (RSA, UC, WTU). Winkler Co.: 1 mi N of southern county line on highway 18, *Irving 69* (SMU, TEX).

MEXICO. COAHUILA: Morillo, Saltillo, *Lyonnet 3497* (US). Saltillo, *Fisher in 1926* (DS). 6 mi N of La Ventura, *Johnston 7644 & Shreve 8726* (ARIZ, UC, US). NUEVO LEÓN OR COAHUILA: Vanegas-Saltillo road, alkali plain, *Lundell 5721* (ARIZ, F, POM). CHIHUAHUA: 13 mi S of Gallegos, *Breedlove 15734* (DS). ZACATECAS: Intersection of highways 49 and 45, *Cruden 1238* (TEX). No locality: Mexico, *Gregg 33* (MO).

Calylophus hartwegii subsp. *filifolius*, which is largely endemic to gypsum soils, may include some convergent populations of independent origin. The Texas and Coahuila populations are widely separated, with no collections having yet been obtained in the intervening region, a span of over 650 km.

I have retained here certain populations with broader leaf dimensions than were included by Shinners or Munz. Plants from the type locality do not all have filiform leaves, although collections from the White Sands area do include the narrowest-leaved plants in the species. Inclusion of the broader-leaved populations here simplifies the variation pattern in *C. hartwegii* subsp. *hartwegii* and renders subsp. *filifolius* a major geographical race which is nonetheless phenetically discrete. In West Texas and southeastern New Mexico this taxon is abundant on plains at about 600–1,200 m elevation. Some variability is shown by this subspecies in terms of leaf width, petal shape, the presence and distribution of anthocyanins, and length of the free sepal tips. Pubescence is relatively uniform, with nearly all plants being glandular-pubescent, and only a few being even minutely strigulose.

The pollination studies of Gregory (1964; as *Oenothera hartwegii*) in Ector and Ward cos., Texas indicated that flowers of *C. hartwegii* subsp. *filifolius* were

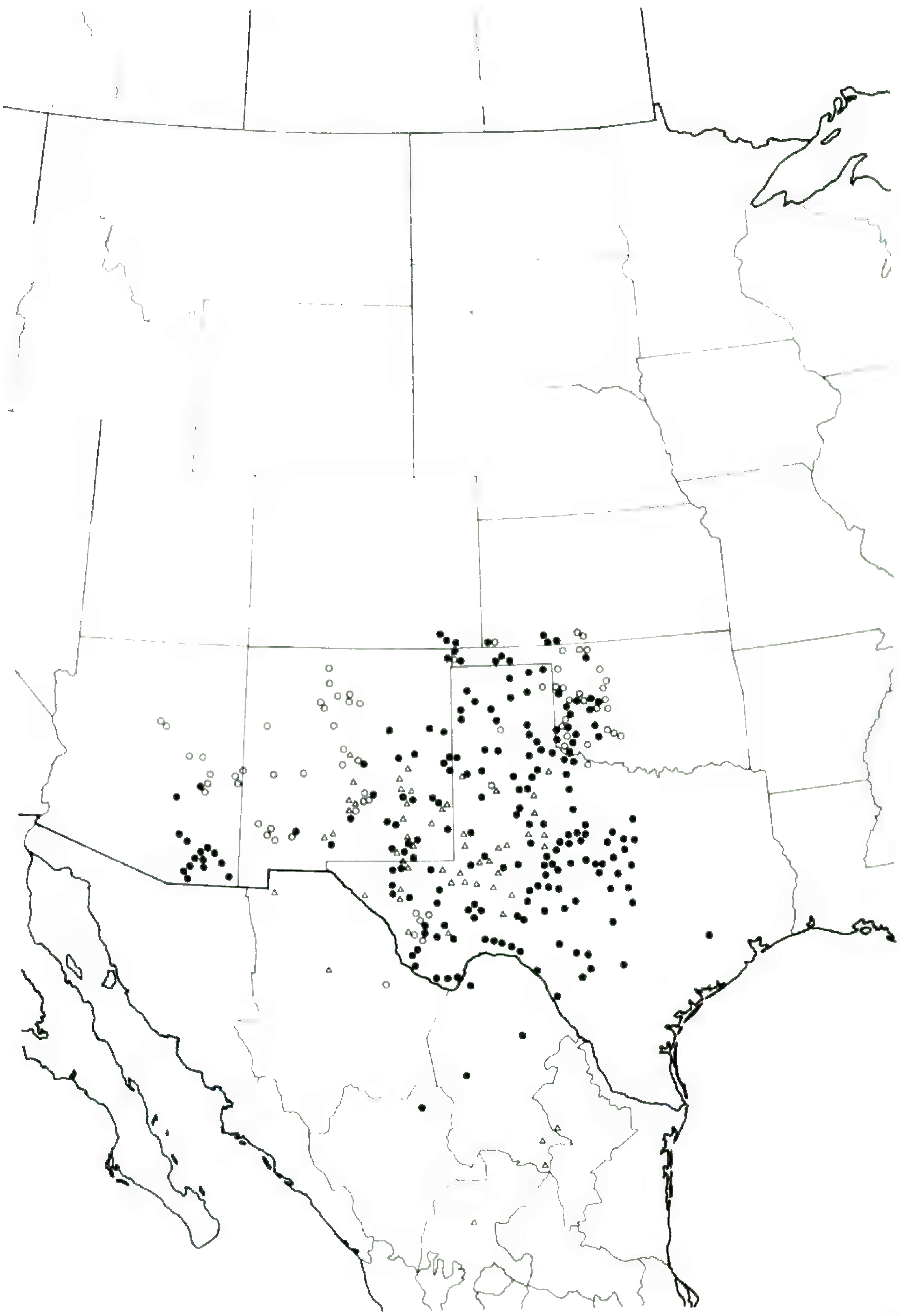


FIGURE 16. Distributions of *Calylophus hartwegii* subsp. *pubescens* (dots), *C. hartwegii* subsp. *fendleri* (open circles), and *C. hartwegii* subsp. *filifolius* (triangles).

open well before sunset and were visited by hawkmoths in the evening and sometimes by bees in the afternoon. Greenhouse studies showed anthesis to occur 3–6 hours before sunset. Ultraviolet-absorbing spots at the base of each petal were fairly large, presenting conspicuous regions of high contrast which would be visible to diurnal insects. Tests for self-incompatibility on 6 plants all proved positive.

Cytogenetically, *C. hartwegii* subsp. *filifolius* exhibits a great deal of variation, with plants averaging 1.7 translocation heterozygosities. Ten of 12 plants from 8 populations were heterozygous. The maximum association of chromosomes observed consisted of a ring of 12 and a bivalent, present in a plant grown from seed collected in Winkler Co., Texas (*Irving 69*). As many as 11 extra diminutive chromosomes were observed in plants from that population, with some being possessed by each of the 4 plants examined. No other population demonstrated extra chromosomes, and no tetraploid or higher counts were obtained from this subspecies. One possible intermediate between *C. hartwegii* subspp. *maccartii* and *filifolius*, as mentioned before, was tetraploid (*Towner 39*). Crosses of *C. hartwegii* subsp. *filifolius* with other forms in sect. *Salpingia* demonstrated complete homology with *C. tubicula*, *C. hartwegii* subsp. *fendleri*, and *C. hartwegii* subsp. *pubescens*, and one or two translocation differences from the other taxa.

Calylophus hartwegii subsp. *filifolius* intergrades somewhat with *C. hartwegii* subsp. *fendleri* in the southern Texas Panhandle and in New Mexico, but hybridization is limited by the altitudinal separation of these subspecies. Similarly, there is limited hybridization with *C. hartwegii* subsp. *pubescens* in the same regions. Possible hybridization with *C. hartwegii* subsp. *maccartii* and *C. hartwegii* subsp. *hartwegii* was treated under those taxa. Sympatry without hybridization occurs in New Mexico where *C. berlandieri* and *C. serrulatus* occasionally come into contact with this subspecies.

1d. **Calylophus hartwegii** (Benth.) Raven subsp. **fendleri** (A. Gray) Towner & Raven, Madroño 20: 243. 1970.

Oenothera fendleri A. Gray, Mem. Amer. Acad. Arts., n.s., 4: 45. 1849. *O. hartwegii* Benth. var. *fendleri* (A. Gray) A. Gray, Pl. Wright. 2: 58. 1853. *Galpinsia hartwegi* (Benth.) Britton (var.) *fendleri* (A. Gray) Small, Bull. Torrey Bot. Club 23: 186. 1896. *G. fendleri* (A. Gray) Heller. Cat. N. Amer. Pl., ed. 2: 8. 1900.

Oenothera hartwegii Benth. var. *typica* sensu Munz, Amer. J. Bot. 16: 706. 1929, pro parte. *Calylophus hartwegii* (Benth.) Raven var. *hartwegii* sensu Shinners, Sida 1: 342. 1964, pro parte. *Oenothera hartwegii* var. *hartwegii* sensu Munz, N. Amer. Fl., ser. 2, 5: 139. 1965, pro parte.

Stems one to several, sparingly to moderately branched above, ascending to more or less erect, 1.5–4 dm high; plant glabrous throughout, infrequently minutely and sparingly glandular-pubescent. Leaves sparse to dense on stems, more or less ascending, linear to oblanceolate or lanceolate, 10–50 mm long, 1.5–10 mm wide, the tip acute, the base acute-attenuate to obtuse, infrequently nearly clasping, the margin entire to subentire, infrequently undulate; axillary leaves usually absent, to 10 mm long when present. Floral tube 30–50 mm long,

7–15 mm wide at the throat, sometimes with purple lines, frequently fading purplish or orange. Sepals 9–28 mm long, 4–10 mm wide, with free tips 0.5–3 mm long, occasionally with purple margins or spotting. Petals obovate to somewhat rhomboidal or squarish, 10–30 mm long, usually fading purplish or reddish, with a basal ultraviolet-absorptive spot small or absent. Filaments 5–12 mm long; anthers 5–13 mm long. Style 40–75 mm long, glabrous above, minutely pubescent basally; stigma 2–6 mm broad; ovary 7–20 mm long, 1–2 mm wide. Capsule 10–40 mm long, 2–3 mm wide; seeds 1–1.5 mm long. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. NEW MEXICO: without specific locality, "probably Santa Fe," 1847, *A. Fendler 230* (GH, lectotype; GH, MO, NY, P, PH, US, isolectotypes); cf. Munz, Amer. J. Bot. 16: 708. 1929. The sheets assigned this number are probably a mixture of collections from the originally published localities, i.e., Santa Fe, on the Río del Norte (Rio Grande), and from Rock Creek eastward to the Cimarron River.

Distribution (Fig. 16); Uncommon on clay or gravelly soils, occasionally calcareous, from high plains with *Prosopis glandulosa* and *Juniperus*, to montane forests with *Juniperus*, *Pinus edulis*, and occasionally *Pinus ponderosa*, from Barber and Morton cos., Kansas, south through western Oklahoma and widely scattered sites in the Texas Panhandle to eastern Chihuahua, central Trans-Pecos Texas, central and western New Mexico, and east-central Arizona. Elevational distribution from ca. 370 m (Agawam, Grady Co., Oklahoma) to 2,200 m (17 mi N of Alpine, Apache Co., Arizona). Flowers April to October.

Representative specimens examined:

UNITED STATES. KANSAS: Barber Co.: NW corner of county, *Baker in 1904* (NY). Gypsum hills, *Hitchcock 689* (GH, NMC, NY, RM, US). 6 mi W of Medicine Lodge, *Stephens 11150* (KANU, OKLA). 7 mi W of Medicine Lodge, *McGregor 14243* (KANU, SMU, US). 7 mi SW of Medicine Lodge, *McGregor 14472* (SMU, US). Sandy soil S of Coats, *Bondy in 1936* (ARIZ, CAN, F, MO, OKL, OKLA, RM). 7 mi S of Sun City, *McGregor 14019* (KANU). Morton Co.: 4 mi W of Rolla, *McGregor 12858* (KANU, SMU, US). OKLAHOMA: Blaine Co.: 5 mi NE of Watonga, *Stephens & Brooks 20819* (KANU). Roman Nose State Park, *Goodman & Waterfall 4185* (GH, OKL, OKLA). Grady Co.: 8 mi SW of Chickasha, *Pearce 767* (SMU). Greer Co.: 7.7 mi S of Mangum, *Towner 79* (DS). 2.6 mi S of Mangum, *Towner 85* (DS). 0.5 mi S and 4.3 mi W of Brinkman, *Towner 86* (DS). Harmon Co.: 10 mi S of McQueen, *Stephens & Brooks 20758* (DS, KANU). Harper Co.: Near Buffalo, *Stevens 535* (DS, GH, MO, NY, OKL, OKLA, US). 17 mi E and 7 S of Buffalo, *Stephens & Brooks 21685* (DS, KANU). Kiowa Co.: Snyder, *Stevens 1198* (OKLA). Roger Mills Co.: 18 mi N of Cheyenne, *Waterfall 11897* (OKLA, SMU, TEX, US). Ca. 8 mi E of Strong City, *Towner 156* (DS). Woods Co.: 37 mi W of Alva, *Stratton 6384* (KANU, OKL). Woodward Co.: 24 mi N of Mooreland, *Brooks & Stephens 21658* (DS, KANU). TEXAS: Hemphill Co.: Prairies N of Canadian, *Eggert in 1901* (MO). Jeff Davis Co.: 14.8 mi N of Marfa city limits, *Parnell 68-T-30* (DS). 8 mi S of Fort Davis, *Munz & Gregory 23384* (RSA, UC). 3.8 mi W of Fort Davis, *Gregory 134* (NY, RSA, WTU). Mesa S of Fort Davis, *Andrews 63* (COLO, GH). Limpia Canyon, Davis Mts., *Bray in 1902* (TEX). Presidio Co.: 8 mi E of Marfa, *Warnock 7916* (LL, SMU, TEX). 8 mi NW of Marfa, *Jackson in 1964* (progeny only, DS). 13.0 mi NW of Marfa, *Towner 25* (DS). 11.9 mi NW of Marfa, *Towner 26* (DS). 10.4 mi NW of Marfa, *Towner 27* (DS). Randall Co.: Bottom of canyon, Palo Duro Canyon State Park, *Lundell & Lundell 11442* (LL, SMU). Wilbarger Co.: 1.5 mi S of Harrold, *Whitehouse 9764* (ARIZ, SMU, UC, US). NEW MEXICO: Catron Co.: Mangas Creek, *Rusby in 1880* (US). Mangas Canyon, *Greene in 1880* (F, MO, NY, PH). Grant Co.: Vicinity of Gila, *Maguire 11630* (DAO, NY, WTU). Lincoln Co. (?): Gallinas Mts., *Wooton 2741* (US). Otero Co.: 8 mi E of Mescalero, *Parker 2556a* (ARIZ, COLO). Above Mescalero, White Mts., *Wooton in*

1895 (US). Rio Arriba Co.: Arroyo de Agua, *Gregory 588* (UC). Sandoval Co.: San Isidro, *Benedict 2311* (US). San Miguel Co.: Near Pecos, *Standley 4952* (GH, MO, NMC, NY). Santa Fe Co.: 19 mi W of Santa Fe, along the Rio Grande R., *Heller & Heller 3622* (MO, NY, US). Socorro Co.: 0.4 mi S of Magdalena, *Towner 119* (DS). Torrance Co.: 3.1 mi NW of Cedarvale, *Towner 123* (DS). 2.6 mi W of Willard, *Towner 121*. Valencia Co.: 8 mi E of Ramah, *Wooton in 1906* (NMC, NY, US). ARIZONA: Apache Co.: 17 mi N of Alpine, *Breedlove 14298* (DS). 7.9 mi N of Alpine, *Towner 110* (DS). 4.5 mi N of Nutrioso, *Towner 111* (DS). 8.0 mi N of Nutrioso, *Towner 112* (DS). Coconino Co.: Walnut Canyon, *MacDougal in 1898* (ARIZ, F, GH, NY, PH, RM, UC, US). Flagstaff Cemetery, *Demaree 42847* (ARIZ, DS, OKLA, RSA, SMU). Navajo Co.: Near Heber, *Parker et al. 6832* (ARIZ, F). 12 mi N of Whiteriver, *Goodman & Hitchcock 1298* (DS, F, MO, NY, PH, UC).

MEXICO. CHIHUAHUA: 11 mi E of Highway 16 on road to new lake on Río Conchos, *Powell et al. 2032* (TEX).

A race with distinctive characters of distribution, morphology, and floral behavior, *Calylophus hartwegii* subsp. *fendleri* definitely merits recognition, contrary to the opinion of Shinners (1964). Late anthesis, glabrous vegetative parts, and distribution at relatively high altitudes or latitudes are strongly correlated in this form. In the northern part of its range, it occurs at intermediate or low altitudes, but in Arizona and New Mexico it ranges up into the coniferous forests. Leaf dimensions not being of critical importance for delimiting this subspecies has allowed the inclusion of elements from Munz's *Oenothera hartwegii* var. *hartwegii*. Thus considerable variation in leaf dimension is retained in *C. hartwegii* subsp. *fendleri*, which attains a large and broad leaf size for the species, especially in collections from the Great Plains. Relatively narrow-leaved forms from the mountains of Trans-Pecos Texas belong here, although they have been traditionally placed with *Oenothera hartwegii* var. *hartwegii*.

The type series of *Evylaeus galpinsiae* (Cockerell) was collected from *Calylophus hartwegii* subsp. *fendleri* near Pecos, New Mexico where the bees were active at 7:30 in the evening (Cockerell, 1903). Pollination studies of Gregory (1964) in Jeff Davis Co., Texas (as *Oenothera hartwegii*) suggested that anthesis occurs near sunset and that pollination is largely accomplished by hawkmoths. My field observations in Grant Co., New Mexico (*Towner 244*) differed somewhat from Gregory's in that numerous bees of the genera *Sphecodogastra* and *Evylaeus* were active gathering pollen from this subspecies for about one hour starting at sunset. As observed by Gregory, hawkmoths visited the flowers heavily in the early evening. Infrequent visits by bees were seen in the morning. Field observations at this site and elsewhere in New Mexico indicated that anthesis occurs at about sunset, and flowers on cultivated plants opened within an hour before or after sunset. Photography under ultraviolet light showed plants to have either no spots of absorption on the petals or only very small ones (Fig. 10). Two plants were checked and found to be self-incompatible.

No tetraploid individuals have been found in this subspecies. Sixteen of 23 plants from 12 of 15 populations were heterozygous for translocations, with a mean number of 0.9 heterozygosities per plant. The maximum number of heterozygosities exhibited was 2, seen in 5 plants. Hybrids with other taxa in sect. *Salpingia* behaved identically to those involving *C. hartwegii* subsp. *filifolius* in terms of chromosome pairing. Four to 5 extra diminutive chromosomes were observed in 3 plants, each from a different population.

Instances of hybridization with *C. hartwegii* subsp. *pubescens*, particularly in

Oklahoma, seem relatively common, and the two subspecies are not separated by large ecological differences. One population in Harmon Co., Oklahoma consisted of both subspecies and intermediates. Cases of intergradation with other taxa have been discussed in previous sections. *Calylophus hartwegii* subsp. *fendleri* occurs frequently with *C. serrulatus* in Oklahoma, with no indication of hybridization. A population in Torrance Co., New Mexico was found growing with *C. lavandulifolius*, and again no intermediates or putative hybrids were observed.

1e. **Calylophus hartwegii** (Benth.) Raven subsp. **pubescens** (A. Gray) Towner & Raven, Madroño 20: 243. 1970.

Oenothera greggii A. Gray var. *pubescens* A. Gray, Pl. Wright. 1: 72. 1852. *Calylophus hartwegii* (Benth.) Raven var. *pubescens* (A. Gray) Shinners, Sida 1: 344. 1964.

Oenothera greggii A. Gray, Mem. Amer. Acad. Arts, n.s., 4: 46. 1849. *Galpinsia greggii* (A. Gray) Small, Bull. Torrey Bot. Club 23: 186. 1896. *Oenothera hartwegii* Benth. var. *fendleri* (A. Gray) A. Gray subvar. *filifolia* H. Lév. f. *thymifolia* H. Lév., Monogr. Onoth. 335. 1908, based on MO isotype. *O. greggii* var. *typica* Munz, Amer. J. Bot. 16: 709. 1929. TYPE: Mexico, Durango, hill SE of Pelayo, ca. 60 mi NW of Torreón, 8 May 1847, *Josiah Gregg 591* (GH, holotype; MO, NY, isotypes).

Oenothera lampasana Buckley, Proc. Acad. Nat. Sci. Philadelphia 1861: 454. 1961. *Galpinsia lampasana* (Buckley) Wooton & Standley, Contr. U.S. Natl. Herb. 16: 152. 1913. *Oenothera greggii* A. Gray var. *lampasana* (Buckley) Munz, Amer. J. Bot. 16: 710. 1929. TYPE: United States, Texas, Lampasas Co., prairies, 1860–1861, *S. B. Buckley* (PH).

Galpinsia interior Small, Fl. S.E. U.S. 845, 1335. 1903. TYPE: United States, Nebraska, Cherry Co., Fort Niobrara, 25 June 1888, *T. E. Wilcox* (NY). This locality is more than 300 mi N of the known range of this subspecies and probably resulted from dispersal by accident or human intent, or the label may have been switched.

Galpinsia camporum Wooton & Standley, Contr. U.S. Natl. Herb. 16: 152. 1913. *Oenothera camporum* (Wooton & Standley) Tidestrom in Tidestrom & Kittell, Fl. Ariz. & N. Mex. 278. 1941. TYPE: United States, New Mexico, Lea Co., Knowles, 29 July 1890, *E. O. Wooton* (US-564592, holotype; NMC, POM, US, isotypes).

Stems several, moderately branched above, decumbent to more or less erect, 1–5 dm high; plant usually covered throughout with long spreading trichomes, most densely on the ovary, inflorescence, and upper stem, occasionally also with short glandular or nonglandular trichomes. Leaves somewhat sparse to dense on the stem, most commonly spreading to reflexed downward, sometimes more or less ascending, very narrowly elliptic or narrowly lanceolate to ovate, 5–40 mm long, 1.5–12 mm wide, the tip acute, the base acute to truncate or subcordate and clasping, the margin entire to sparsely serrulate, occasionally undulate-crinkled; axillary leaves often absent or much reduced, occasionally to 15 mm long. Floral tube 20–50 mm long, 4–20 mm wide at the throat, only rarely with purple stripes, occasionally fading purplish. Petals obovate to somewhat rhomboidal or squarish, 12–35 mm long, frequently fading pinkish or purplish, with a basal ultraviolet-absorptive spot of small or moderate size. Filaments 5–12 mm long; anthers 4–13 mm long. Style 25–70 mm long, glabrous above, minutely pubescent basally; stigma 1.5–5 mm broad; ovary 5–30 mm long, 1–3 mm wide. Capsule 6–35 mm long, 2–3 mm wide; seeds 1–1.7 mm long. Self-incompatible. Gametic chromosome numbers, $n = 7, 14$.

TYPE: UNITED STATES. TEXAS: dry hills beyond the Pecos River, probably from Pecos Co., August 1849, *Charles Wright 199* (GH, holotype; GH, NY, PH,

US, isotypes). The locality was calculated from the dates and account of Wright's trip given by McKelvey (1955: 1067–1068).

Distribution (Fig. 16): Common and colonial in moderately dry open places, plains, and hills, in sandy to gravelly soil, often of limestone or gypsum, frequently with *Prosopis glandulosa* and *Juniperus*, from Baca Co. and eastern Las Animas Co., Colorado and Morton and Meade cos., Kansas, to western Oklahoma and the Texas Panhandle, throughout central and Trans-Pecos Texas, thence west through eastern and southern New Mexico to central and southeastern Arizona; also south very locally in central Coahuila and northeastern Durango. Elevational distribution from 200 m (10.5 mi E of Weatherford, Parker Co., Texas) to 2,100 m (2.4 mi NW of Corona, Torrance Co., New Mexico). Flowers March to October.

Representative specimens examined:

UNITED STATES. COLORADO: Baca Co.: 20 mi S of Pritchett, *Harrington 3325* (RSA). 27 mi S of Pritchett, *Weber 4608* (COLO, UC, WTU). Las Animas Co.: 7 mi S and 16 E of Kim, *Weber 4387* (COLO). 4 mi W of Andrix, *Rogers 4952* (COLO, US). KANSAS: Clark Co.: 10 mi S of Ashland, *Rydberg & Imler 744* (NY). Meade Co.: 8 mi S and 7 E of Meade, *Horr in 1957* (KANU). SE corner of county, above Wolf Canyon, *Horr 3612* (KANU). Morton Co.: Stony hills, *Hitchcock 166* (GH, MO, NMC, NY, POM, RM, US). Point of Rocks, *Hitchcock 634* (GH). On Cimarron R., N of Elkhart, Point of Rock, *Rydberg & Imler 942, 943* (MO, NEB, NY). Point of Rocks, 7 mi N and 4 W of Elkhart, *Stephens 11258* (KANU). No county: SW Kansas, *Plank in 1886* (GH). OKLAHOMA: Beckham Co.: 8 mi N of Sayre, *Wiedman in 1959* (OKL, OKLA). 6 mi S of Elk City, *Eskew 1503* (GH, KANU, OKL, OKLA). 1.7 mi W and 2.4 N of Elk City, *Stratton 6835* (KANU, OKLA). Cimarron Co.: 16 mi SE of Kenton, *Waterfall 7433* (OKL, OKLA, TEX). 2 mi N of Kenton, *Hopkins & van Valkenburgh 5754* (NY, RM, SMU). Custer Co.: 1 mi W and 0.3 S of Weatherford, *Waterfall 442* (OKLA, POM). Canyon rims, Clinton, *Demaree 12466* (ARIZ, GH, MO, NY, OKL, PH, POM, SMU, US). 10 mi W of Clinton, *Munz & Gregory 23508* (RSA). Ellis Co.: Near Shattuck, *Clifton 3174* (GH, OKLA). Greer Co.: 2 mi S of Mangum, *Robbins 3038* (NY, OKL). 3 mi S of Mangum, *Stephens 20812* (DS). 4.5 mi S of Mangum, *Towner 82* (DS). Harmon Co.: Near Hollis, *Stevens 1162* (DS, GH, MO, NY, OKL, OKLA, US). 13.5 mi W of Mangum, *Waterfall 7174* (OKL, OKLA). Jackson Co.: 3 mi N and 1 W of Eldorado, *Waterfall 9008* (OKL, OKLA). Kiowa Co.: 3 mi W of Gotebo, *Goodman 6274* (OKL, RSA, UC). Roger Mills Co.: Red lands, *Engleman 417, 418* (OKL). 2.5 mi S of Cheyenne, *Wiedeman 183* (OKL, OKLA). Texas Co.: Goodwell, *Butler 85* (OKLA). 5.5 mi E of Hardesty, *Stephens & Brooks 21775* (DS). 7 mi NE of Texhoma, *Waterfall 9123* (GH, OKL, OKLA). TEXAS: Brewster Co.: Glass Mts., *Tharp 3629* (US). 4 mi S of Alpine, *Munz & Gregory 23395* (RSA, UC). Hot Springs area, *Sperry 1732* (GH). 3.3 mi W of Alpine, *Towner 28* (DS). Brown Co.: 8.2 mi S of Brownwood, *Towner 63* (DS). Callahan Co.: Ca. 17 mi SE of Abilene, *Henderson 64-53* (DS). Coke Co.: 5.2 mi SE of Bronte, *Raven & Gregory 19279* (DS). Coleman Co.: 14.3 mi N of Coleman, *Towner 75* (DS). Comanche Co.: 2 mi E of Comanche, *Deckmeier 17* (LL, SMU, TEX). Concho Co.: 2.5 mi W of Eden, *Munz & Gregory 23425* (RSA, UC, WTU). 2.8 mi N of Eden, *Raven & Gregory 19277* (DS). Culberson Co.: 27 mi SW of White's City, New Mexico, *Munz & Gregory 23364* (RSA, UC). 10 and 12 mi N of Van Horn, *Waterfall 4095* (ARIZ, GH, MO, NY). Victoria Canyon, Sierra Diablo, *Correll & Rollins 23783* (LL). 25.6 mi SW of White's City, New Mexico, *Towner 23* (DS). Glasscock Co.: 3 mi E of Garden City, *Munz & Gregory 23420* (RSA, UC, WTU). Hardeman Co.: 1 mi N of Quanah, *Stephens 20721* (DS). Irion Co.: 30 mi N of Barnhart, *Raven & Gregory 19211* (DS). Lampasas Co.: Lampasas, *Reverchon 1302* (DS, F, MO, NY, PH, UC, US). Maverick Co.: Eagle Pass, *Havard s.n.* (US). Mills Co.: 0.9 mi N of center of Goldthwaite, *Towner 70* (DS). Pecos Co.: 25 mi NW of Sanderson, *Munz & Gregory 23405* (RSA, UC, WTU). Potter Co.: 3.1 mi N of U.S. 66 on Farm Road 1719, *Towner 93* (DS). 11.3 mi N and 3.9 W of central Amarillo, *Towner 192* (DS). Presidio Co.: Ca. 35 mi S of Marfa, Bunton Flats, *Warnock 46621* (RSA). Ca. 3 mi SW of Marfa, *Hinckley 706* (LL). 12 mi N of Shafter, *Scuddy 396* (OKLA). Marfa, *Eggleston 17341* (US). Real Co.: Leakey, *Palmer 10149* (DS, PH, POM). Roberts Co.: 24 mi

S of Perryton, *Anderson 2988* (KSC). Taylor Co.: Camp Barkeley, *Tolstead 7065* (MO, SMU, UC). Terrell Co.: 6.7 mi E of Sanderson, *Raven & Gregory 19202* (DS). 6.3 mi E of Sanderson, *Gregory 275* (DAO, RSA, UC). 9.6 mi W of Dryden, *Parks et al. 305* (LL, SMU). Uvalde Co.: Sabinal, *Palmer 11514a* (MO). By Sabinal R., *McKelvey 1879* (GH, POM). Uvalde, *Dobie in 1930* (TEX). Val Verde Co.: Pumpville turnoff, *Warnock 11313* (LL, SMU). Ca. 5 mi W of Langtry, *Warnock & Cameron 9937* (LL, SMU). Ward Co.: Near Monahans, *Wheeler in 1938* (LL). Wheeler Co.: Ca. 0.5 mi W of Shamrock, *Towner 88* (DS). Counties unknown: Near Mt. Carmel, Rio Grande, *Parry 369* (NY, PH). On the Rio Grande, *Wright in 1848* (MO). Between Austin and Stephensville, *Kagan in 1966* (TEX, biochemical voucher). NEW MEXICO: Chaves Co.: Ca. 5 mi N of Roswell, *Towner 126* (DS). 13.5 mi W of Hope, *Towner 13* (DS). Ca. 8 mi E of Elk, *Towner 12* (DS). De Baca Co.: N side of Fort Sumner, *Shinners 20922* (SMU). Dona Ana Co.: Organ Mts., *Wooton in 1900* (NMC, POM, RM, US). Eddy Co.: Near Three Forks of Rocky Arroyo, Guadalupe Mts., *Wilken 1734* (PH, US). 1.5 mi ENE of headquarters, Carlsbad Caverns National Park, *Dole 74* (UC). Junction of Delaware Creek and Pecos R., *Pope in 1835* (GH). Memorial Hospital, N end of Carlsbad, *Munz & Gregory 23355* (RSA, UC). Lea Co.: 1–11 mi N of Hobbs, *Pearce 2569* (ARIZ). 60 mi E of Roswell, *Palmer 66* (F). Lincoln Co.: Ca. 15 mi W of Roswell, *Dunn 8700* (RSA). 10 mi E of Capitan, *Hitchcock et al. 4201* (DS, UC, WTU). Hando (Hondo?) Hill, *Wooton in 1904, 1906* (NMC). Otero Co.: 9 mi NE of Alamogordo, *Munz & Gregory 23337* (RSA, UC, WTU). Quay Co.: Ca. 9 mi W of Tucumcari, *Towner 94* (DS). 8 mi SW of Tucumcari, *Shinners 21062* (SMU). 8 mi S of San Juan, *Stephens & Brooks 25573* (DS). Roosevelt Co.: Portales Springs, *Martin 784* (WTU). Near Causey, *Wooton in 1909* (NMC). Sierra Co.: Berendo Creek, *Metcalfe 1574* (F, GH, MO, NMC, NY, POM, UC, US). Torrance Co.: 2.4 mi NW of Corona, *Towner 124* (DS). Union Co.: Ca. 4 mi N of Moses, *York & Rodgers 147, 149* (SMU, TEX). ARIZONA: Cochise Co.: 15 mi E of Bernardino, *Benson 10284* (ARIZ, POM, UC). 6 mi NW of Chiricahua, *Gould & Pultz 3155* (ARIZ, GH, UC). 6 mi W of entrance to Chiricahua National Monument, *Gregory 408, 411* (DAO, DS, RSA, UC, WTU). 3 mi E of Dos Cabezas, *Maguire 11152* (DAO, GH, NY, UC, WTU). Mescal (ca. 7 mi W of Benson), *Thornber 4312* (ARIZ, OKLA, SMU). Dragoon, *Trogstadt 1068* (ARIZ, NMC). Ca. 3 mi E of Cochise Stronghold, Dragoon Mts., *Towner 161* (DS). Gila Co.: 1 mi N of Black R., San Carlos Indian Reservation, *Goodman & Hitchcock 1287* (DS, F, MO, NY, PH, POM, UC). 1 mi N of Blackriver Road, *Granfelt in 1960* (ARIZ). Between Globe and Cooley (Coolidge?), *Nelson 10372* (DS, MO, NY, mixture with *C. lavandulifolius*). Pima Co.: Redington, *Goodding in 1935* (ARIZ). Tucson-Redington Road, San Pedro Valley, *Brass 14282a* (GH, NY). Pinal Co.: Near Oracle, Santa Catalina Mts., *Lewis 1079* (RSA, UC). Peppersauce Canyon, Santa Catalina Mts., *Darrow in 1937* (NY). Hills near Oracle, *Harrison & Kearney 6673* (US). 7.7 to 7.9 mi SE of Oracle, Santa Catalina Mts., *Towner 1, 3* (DS). Santa Cruz Co.: Mustang Mts., *Pringle in 1884* (F, GH, MO, NY, POM, US). Near Sonoita, *Harrison & Kearney 5713* (ARIZ, US). Sonoita to Elgin, *Peebles & Fulton 11485* (ARIZ, US). 7.5 mi E of Sonoita, *Gregory 404, 405* (DAO, RSA, UC). 7.5 mi SE of Sonoita on road to Canelo, *Towner 105* (DS).

MEXICO. COAHUILA: Santa Rosa Mts., *Marsh 1338, 1491* (F, OKLA, SMU, TEX). 27 mi E of Boquillas, *Henrickson 11611b* (TEX). 64 mi W of Cuatro Cienegas, *Henrickson 7861* (TEX). 4.5 km E of Matrimonio Viejo, *Johnston 10895* (TEX).

Most abundant of the races of this species, *Calylophus hartwegii* subsp. *pubescens* occurs widely in Texas and neighboring states. In central Texas, it is the only member of sect. *Salpingia*. Spreading trichomes and broad truncate-based leaves are strongly correlated in this form, and are characteristic of the central Texas populations and most others which are not affected by introgression. The type of *Oenothera greggii* is tentatively included here, although the plants are stunted and somewhat lacking in distinctive characters. They are not typical of *C. hartwegii* subsp. *pubescens* and may represent hybrids or introgressants with subsp. *hartwegii*, which also occurs in that region. For these reasons, I have followed Shinners' (1964) decisions and taken up the epithet "*pubescens*" for this taxon.

Calylophus hartwegii subsp. *pubescens* is one of the most variable taxa in *Calylophus*, much of this perhaps stemming from the influence of introgression. The size of the flowers and of leaves and other vegetative parts all vary widely. Leaf margins may or may not be crinkled. Pubescence may consist wholly of spreading hairs or of these combined with shorter glandular or nonglandular pubescence. These characters appear to vary in response to genetic exchange with subspp. *filifolius* and *hartwegii*.

Records of pollinators reported by Gregory (1964; as *Oenothera greggii*) in Terrell Co., Texas and Cochise Co., Arizona, included hawkmoths in the evening at both sites (*Hyles lineata*, *Manduca quinquemaculata*, *Sphinx dolli*) and bees in the morning at the Cochise Co. site (*Megachile*, *Melissodes*, *Bombus*). On a different date at the same locality in Arizona, I observed numerous halictid bees (*Dialictus*, *Agapostemon*, *Evylaeus*) and some bumblebees (*Bombus*) gathering pollen in the late afternoon. In the evening, hawkmoth (*Hyles lineata* and *Manduca quinquemaculata*) visitation was frequent. My field and greenhouse observations showed a range in anthesis times extending from 2 hours before sunset to about sunset. Thus flowers in this subspecies may not always be open early enough for significant afternoon visitation by bees. Ultraviolet-absorbing regions on the petals were found to be of small to moderate size. Each of four plants that were artificially pollinated was found to be self-incompatible.

Tetraploidy and translocation heterozygosity are present in *C. hartwegii* subsp. *pubescens*, with tetraploidy occurring in one (Pecos Co., Texas, *Munz & Gregory 23405*) of the 18 populations which have been examined. A population intermediate between subsp. *pubescens* and subsp. *hartwegii* (Brewster Co., Texas, *Munz & Gregory 23401*) was also found to be tetraploid by Kurabayashi et al. (1962). Interchange heterozygotes comprised 15 of 20 plants examined for meiotic configurations, occurring in 11 of 15 populations. An average of 1.2 translocation heterozygosities per plant was calculated for this form, with a maximum of 3, the most frequent number being 1. No extra diminutive chromosomes have yet been observed in *C. hartwegii* subsp. *pubescens*. Configurations obtained from hybrids with other members of sect. *Salpingia* exhibited 0–2 translocation heterozygosities.

Most instances of introgression have been discussed in earlier sections. Two possible cases of hybridization with *C. lavandulifolius* were discovered for this taxon, perhaps the only subspecies of *C. hartwegii* which hybridizes in nature with *C. lavandulifolius*. One was a sight record from Guadalupe Co., New Mexico, where some plants with slight resemblances to *C. lavandulifolius* were found in two populations of *C. hartwegii* subsp. *pubescens*. The second was a single plant intermediate between the same taxa [between Globe and Cooley(?), Arizona, *Nelson 10372*, (RM)] observed in a mixed collection of the two typical forms. Numerous cases of sympatry without hybridization were observed, especially with *C. serrulatus* in Oklahoma, New Mexico, and the northern Texas Panhandle, and with *C. berlandieri* in central Texas and the Panhandle. Other instances included populations mixed with *C. lavandulifolius* in Culberson Co., Texas and with *C. tubicula* in Chaves Co., New Mexico.

2. **Calylophus lavandulifolius** (Torr. & A. Gray) Raven, Brittonia 16: 286. 1964.

Oenothera lavandulaefolia Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. *O. hartwegii* Benth. var. *lavandulaefolia* (Torr. & A. Gray) S. Wats., Proc. Amer. Acad. Arts 8: 590. 1873. *Galpinsia lavandulaefolia* (Torr. & A. Gray) Small, Fl. S.E. U.S. 845, 1335. 1903. *Oenothera hartwegi* var. *fendleri* (A. Gray) A. Gray subvar. *lavandulaefolia* (Torr. & A. Gray) H. Lév., Monogr. Onoth. 334. 1908. *O. lavandulaefolia* var. *typica* Munz, Amer. J. Bot. 16: 704. 1929. *Calylophus hartwegii* (Benth.) Raven var. *lavandulaefolius* (Torr. & A. Gray) Shinners, Sida 1: 345. 1964. *Oenothera lavandulifolia* var. *lavandulifolia*; Munz, N. Amer. Fl., ser. 2, 5: 138. 1965. *Calylophus hartwegii* subsp. *lavandulifolius* (Torr. & A. Gray) Towner & Raven, Madroño 20: 243. 1970.

Oenothera lavandulaefolia Torr. & Gray var. *glandulosa* Munz, Amer. J. Bot. 16: 705. 1929. *Galpinsia lavandulaefolia* (Torr. & A. Gray) Small var. *glandulosa* (Munz) Moldenke, Phytologia 2: 134. 1946. TYPE: United States, Nevada, White Pine Co., Ely, 30 July 1923, *M. E. Jones* (POM).

Similar to *Calylophus hartwegii.* Suffrutescent perennial from a stout woody caudex, caespitose, sometimes appearing more or less tufted; stems several to many, moderately branched, spreading-decumbent to more or less ascending, 0.4–2(–3) dm high; plant densely gray-strigulose throughout. Leaves dense on the stem, sessile, usually ascending, linear to narrowly lanceolate or narrowly oblanceolate, 6–50 mm long, 0.8–6 mm wide, the tip acute or obtuse, the base acute-attenuate, the margin entire or nearly so, occasionally slightly undulate, infrequently revolute; small axillary leaves present, 2–10 mm long; lowest stem leaves somewhat wider and more oblanceolate than above. Floral tube 25–60 mm long, 5–15 mm wide at the throat, minutely strigulose or glandular-pubescent without, sometimes with purple longitudinal lines and base, occasionally fading pinkish upon wilting. Sepals 8–20 mm long, 3–8 mm wide, with free tips 0.3–3 mm long, usually with purple marginal stripes. Petals 12–28 mm long, similar in width, usually fading pinkish to purplish, highly ultraviolet-reflective, with a small basal ultraviolet-absorptive spot, rarely medium-sized. Filaments 6–12 mm long; anthers 5–11 mm long. Style 30–75 mm long, glabrous above, minutely pubescent below; stigma 2–5 mm broad; ovary 4–16 mm long, 1–2 mm wide. Capsule 6–25 mm long, 1–3 mm wide; seeds 1.5–2.5 mm long. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. On plains, probably along the South Platte River in southwestern Nebraska or northeastern Colorado, June or July 1820, *Edwin James* (PH). The approximate locality was taken from McKelvey (1955: 213–219) and is at the eastern limit of the range of this species.

Distribution (Fig. 17): Local and sparse, on sandy and rocky, often calcareous soil, on high plains and in mountains, frequently with *Juniperus, Pinus monophylla* or *Pinus edulis, Cercocarpus, Artemisia tridentata,* occasionally in lower zones with *Larrea divaricata* or in higher zones with *Pinus ponderosa,* from southern Fall River Co., South Dakota, southeastern Wyoming, and far western Nebraska, through western Kansas, Colorado, eastern and southern Utah, northwestern Oklahoma, and the Texas Panhandle to Trans-Pecos Texas, central Nuevo León, central New Mexico, central Arizona, and east-central and southern Nevada. Occurring from elevations of ca. 600 m (2 mi W of Hays, Ellis Co.,

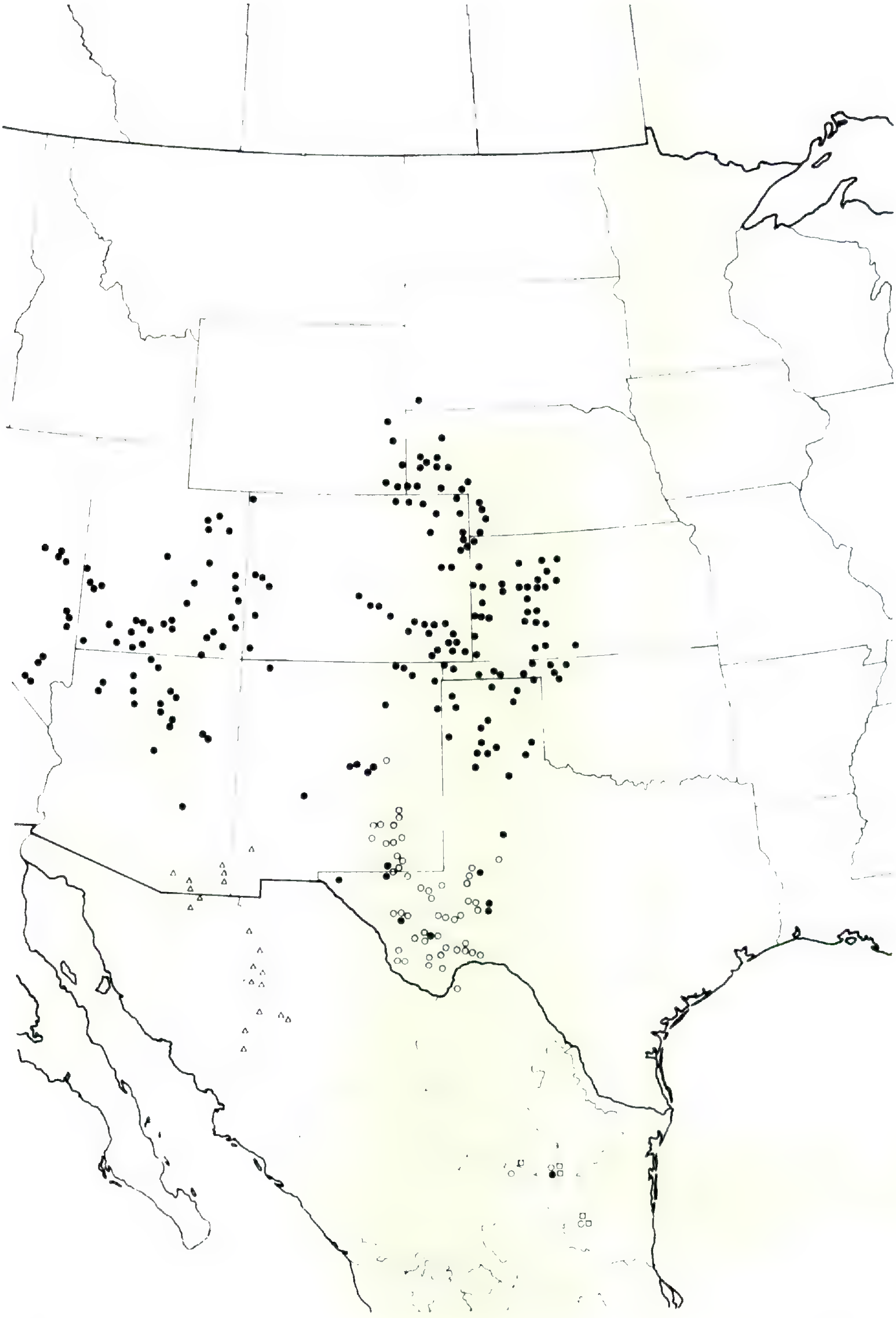


Figure 17. Distributions of *Calylophus toumeyi* (triangles), *C. lavandulifolius* (dots), *C. tubicula* subsp. *tubicula* (open circles), and *C. tubicula* subsp. *strigulosus* (squares).

Kansas) to ca. 2,750 m (Lee Canyon, Spring Mts., Clark Co., Nevada). Flowers April to August.

Representative specimens examined:

UNITED STATES. SOUTH DAKOTA: Fall River Co.: Rocky dry ridges, *Over 18074* (RM). WYOMING: Goshen Co.: 4 mi N of La Grange, *Stephens & Brooks 22903* (DS). Laramie Co.: Hartville, *Nelson 8328* (GH, MO, NY, US). 20 mi W of Pine Bluffs, *Porter & Porter 8153* (DS, POM, UC). SE edge of Pine Bluffs, *Stephens & Brooks 22873* (DS). Platte Co.: Whalen Canyon, *Nelson 526* (GH, MO, NY, US). Near Guernsey, *Porter 3557* (DS, SMU, TEX, UC, WTU). NEBRASKA: Box Butte Co.: 5 mi E and 5 N of Hemingford, *Stephens & Brooks 24542* (KANU). Chase Co.: 10 mi N of Imperial, *Brown 1255* (NEB). Garden Co.: 2 mi S of Lewellen, *Stephens & Brooks 11519* (KANU). Morrill Co.: Angora, *Pool in 1912* (MO, NEB). 4 mi N of Broadwater, *Stephens & Brooks 13907* (DS, KANU). Scott's Bluff Co.: 1.5 mi W and 5 S of Melbeta, *Stephens 5484* (KANU). COLORADO: Baca Co.: 9 mi S and 2 E of Walsh, *Stephens & Brooks 21820* (DS). Bent Co.: 15 mi SE of Las Animas, *Stephens & Brooks 22003* (DS). 4.5 mi W of Prowers, *Stephens & Brooks 21989* (DS). Dolores Co.: Just W of Northdale, *Anderson 3138* (DS). Huerfano Co.: 19 mi NE of Walsenburg, *Stephens & Brooks 22229* (DS). Kit Carson Co.: 5 mi E of Flagler, *Stephens & Brooks 22633* (DS). Las Animas Co.: 6 mi N and 4 E of Andrix, *Stephens & Brooks 21900* (DS). Otero Co.: 2 mi S of Manzanola, *Stephens & Brooks 22315* (DS). Sedgwick Co.: 1 mi S of Julesburg, *Stephens & Brooks 24060* (KANU). KANSAS: Clark Co.: 8 mi N of Ashland, *Horr E248* (COLO, DAO, F, GH, KANU, LL, OKL, RM, SMU, TEX, UC). Ellis Co.: 2 mi W of Hays, *Bondy 77* (ARIZ, F, MO, NMC, OKL, PH, RM, US). Gove Co.: 20 mi S and 3 E of Oakley, *Lathrop 3374* (KANU, SMU). Meade Co.: 12 mi E of Meade, *Horr 3532* (KANU, TEX, US). Morton Co.: 7 mi N and 4 W of Elkhart, *Stephens 8877* (KANU). Scott Co.: Horsethief Canyon, Scott County State Park, *Fearing & Latham in 1950* (GH, KANU). Trego Co.: 14 mi S of Ogallah, *McGregor 17124* (KANU). OKLAHOMA: Beaver Co.: E edge of Elmwood, *Stephens & Brooks 21745* (DS). Harper Co.: 10 mi S of Buffalo, *Goodman 2394* (MO, NY, OKL, POM, UC, WTU). Texas Co.: 5.5 mi E of Hardesty, *Stephens & Brooks 21776* (DS). Woods Co.: Near Freedom, *Stevens 252* (DS, GH, NY, OKL, SMU). TEXAS: Brewster Co.: Foothills of Glass Mts., 7.7 mi NE of U.S. 90 on U.S. 67, *Towner 29* (DS). Culberson Co.: 25.6 mi SW of White's City, E side of Guadalupe Mts., *Towner 24* (DS). Hudspeth Co.: 31 mi E of El Paso, Hueco Mts., *Tharp 46071* (F, MO, TEX). NEW MEXICO: Colfax Co.: Near Raton, *Nelson & Nelson 4681* (DS, RM, US). Eddy Co.: Near Three Forks of Rocky Arroyo, Guadalupe Mts., *Wilkens 1711* (PH). Socorro Co.: Hell Canyon, Magdalena Mts., *Herrick 274* (US). Torrance Co.: 3.0 mi NE of Duran, *Raven 19129* (DS). 5.8 mi SW of Duran, *Raven 19133* (DS). Ca. 7.5 mi W of Willard on U.S. 60, *Towner 120* (DS). ARIZONA: Coconino Co.: Rim of Canyon Diablo, Two Guns, *Demaree 44216* (ARIZ, PH, RSA, SMU). E rim of Canyon Diablo, Two Guns, *Towner 114* (DS). 10 mi SE of Tuba City, *Peebles 13363* (GH, US). 10.9 mi S of Bitter Springs, *Mosquin & Mosquin 4247* (DS). Mojave Co.: Ca. 1 mi from rim of canyon, Toroweap Valley, *McClintock 52-512* (ARIZ, NY). Navajo Co.: 45.0 mi NW of Concho, *Towner 115* (DS). UTAH: Duchesne Co.: Juniper zone, below Moon Lake, *Graham 6412* (MO, POM). Emery Co.: 50 mi N of Hanksville, San Rafael Swell, *Cronquist 9201* (DAO, DS, NY, POM, WTU). Garfield Co.: Red Canyon, 10 mi W of Bryce Canyon, *Preece 2480* (COLO, POM, SMU). Bryce Canyon, *Goodman & Hitchcock 1566* (DS, GH, POM, RM, UC). 10 mi E of Escalante, *Holmgren & Nielsen 7734* (DS, POM, RM, UC, WTU). Millard Co.: Tunnel Springs, Desert Game Range, *Cottam 8553* (ARIZ, POM). San Juan Co.: Tuwa Canyon, Natural Bridges National Monument, *Welsh & Moore 2294* (NY). Uinta Co.: Willow Creek, S of Ouray, *Holmgren 1882* (KANU, WTU). Washington Co.: 10 mi N of the Beaver Dam summit of U.S. 91 and 5 mi NW of the highway, *Wiens 3917* (WTU). NEVADA: Clark Co.: Old Saw Mill site, Sheep Mts., 6,600 ft, *Alexander & Kellogg 1757* (GH, UC, US, WTU). Rocky ridge S of Deer Creek, Charleston (Spring) Mts., 2,670 m, *Clokey & Clokey 7605* (ARIZ, CAN, COLO, DAO, DS, F, GH, KANU, MO, OKL, PH, POM, RM, RSA, SMU, TEX, UC, US, WTU). 4.8 mi N of Kyle Canyon on road to Lee Canyon, Charleston Mts., *Towner 101* (DS). Lee Canyon, 0.7 mi W of jct. to Kyle Canyon, Charleston Mts., *Towner 104* (DS). Lincoln Co.: Panaca Valley and vicinity, *Gentry 131* (ARIZ, DS, UC, US). White Pine Co.: 3 mi S of Ruth, *Moore 346* (DS, POM). 5.1 mi S of U.S. 50, on eastern road to Hamilton, *Raven & Solbrig 13550* (DS). 2 mi W of Ely, *Anderson 2897* (KSC).

MEXICO. NUEVO LEÓN: 15 mi S of San Roberto Junction on Mexico 57, *Sanderson 291, 292* (TEX); *Turner 6357* (TEX). 16 mi S of San Roberto Junction, *Reveal et al. 2652* (DS). Near summit of N.L. Highway 60 W of Galeana, *Sanderson 288*, in part (TEX).

The limits of this species are approximately those given by Munz (1929). Some collections included here by Munz clearly belong with *Calylophus hartwegii* subsp. *hartwegii*, e.g., Zacatecas, gravelly soil, *Purpus in 1903* (UC). The two taxa are easily confused but differ in the shorter sepal tips, denser pubescence, and leaves which are usually broader and obtuse-tipped in *C. lavandulifolius*.

A species of broad distribution, *C. lavandulifolius* occurs for the most part to the north and northwest of the range of *C. hartwegii*. Isolated collections have been made, however, throughout much of the range of the latter. Where *C. lavandulifolius* occurs with *C. hartwegii*, it tends to occupy higher elevations than any race of that species, except for *C. hartwegii* subsp. *fendleri*. Plants of *C. lavandulifolius* are typically slow-growing, small, and sparsely distributed, and are relatively inconspicuous when mixed with populations of the more abundant *C. hartwegii*.

Hybridization with other species of *Calylophus* apparently occurs only rarely. Evidence for gene exchange stems only from the two collections mentioned previously which were intermediate between *C. lavandulifolius* and *C. hartwegii* subsp. *pubescens*. Instances of populations of *C. lavandulifolius* contiguous with those of other taxa have also been mentioned above, and include contact with *C. tubicula* subsp. *tubicula*, *C. tubicula* subsp. *strigulosus*, *C. hartwegii* subsp. *pubescens*, *C. hartwegii* subsp. *fendleri*, and *C. serrulatus*.

Variation within *C. lavandulifolius* is not clearly correlated with geography, and division into subspecies seems inadvisable. The glandular pubescence of the floral tube and calyx used by Munz to distinguish *Oenothera lavandulaefolia* var. *glandulosa* does not appear to vary in any meaningful pattern or in association with any other character. Considerable variation within the species occurs in leaf dimensions, leaf margin (undulate, revolute, or plane), width of the floral tube, and in other floral characters.

Visitors to a population in Clark Co., Nevada (*Towner 195*) consisted entirely of hawkmoths (*Hyles lineata*, *Manduca*), which were active between dusk and dark. Anthophorid and halictid (*Agapostemon*) bees were seen on flowers 2 hours before sunset at a population in Torrance Co., New Mexico (*Towner 120*). Anthesis in the field and greenhouse ranged from 3 hours before sunset to sunset. In the population in Clark Co., Nevada the median time of anthesis was 1½ hours before sunset. Ultraviolet absorption patterns on the petals tend to be small in this species. The foregoing facts suggest that hawkmoth pollination predominates in *C. lavandulifolius*, but that bees may also play a role at certain localities. Two plants were self-pollinated and found to be self-sterile.

Cytological variation in *Calylophus lavandulifolius* occurs in the form of translocations and extra diminutive chromosomes. Seven of 10 plants from 5 of 6 populations were interchange heterozygotes. An average of 1.2 heterozygosities per plant was calculated. Three individuals from separate populations had extra chromosomes, which consisted of 1 or 2 diminutive pairs. Configurations displayed by hybrids of *C. lavandulifolius* with other taxa in sect. *Salpingia* showed 2–3 translocation differences and occasional inversion differences between the

parents, a greater cytological divergence than shown by other crosses within the section.

3. **Calylophus toumeyi** (Small) Towner, comb. nov.—FIGS. 1, 3.

Galpinsia toumeyi Small, Bull. Torrey Bot. Club 25: 317. 1898. *Oenothera hartwegii* Benth. var. *toumeyi* (Small) Munz, Amer. J. Bot. 16: 708. 1929. *O. toumeyi* (Small) Tidestrom, Proc. Biol. Soc. Wash. 48: 41. 1935. *Calylophus hartwegii* (Benth.) Raven var. *toumeyi* (Small) Shinners, Sida 1: 341. 1964. *C. hartwegii* subsp. *toumeyi* (Small) Towner & Raven, Madroño 20: 243. 1970.

Similar to *Calylophus hartwegii*. Suffrutescent perennial from a stout woody caudex; stems several, sparingly branched or unbranched above, ascending to erect, 1.5–6(+) dm high; plant subglabrous to minutely strigulose throughout. Leaves sparsely distributed on the stem, sessile, more or less spreading, narrowly lanceolate, 10–35 mm long, 1–7 mm wide, the tip acute, the base acute-attenuate, the margin entire to obscurely and sparsely serrulate, not undulate; conspicuous fascicles of small leaves 2–25 mm long in nonfloriferous axils; lowest stem leaves usually tending towards oblanceolate shape. Floral tube (15–)30–60(–70) mm long, 5–14 mm wide at the throat, yellowish, fading orangish to brick red upon wilting. Sepals 10–25 mm long, 3.5–6 mm wide, with free tips 2–9(–12) mm long, colored as the floral tube. Petals 10–20 mm long, similar in width, intensely lemon yellow, fading orangish to brick red, moderately ultraviolet-absorptive throughout. Filaments 4–12 mm long; anthers 6–10 mm long. Style 35–70(–80) mm long, glabrous above, minutely pubescent below; stigma discoid to squarish, 1.5–4 mm broad; ovary 6–20 mm long, 1–2 mm wide. Capsule 10–50 mm long, 1.5–4 mm wide, thin walled, sometimes almost papery, dehiscent only in the distal half; seeds 2–3 mm long. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. ARIZONA: Cochise Co., Chiricahua Mountains, 25 July 1894, *J. W. Toumey 197* (NY); Munz, Amer. J. Bot. 16: 708. 1929.

Distribution (Fig. 17): Local and uncommon on shaded rocky slopes or disturbed areas in pine-oak forest, from the Santa Rita, Huachuca, and Chiricahua mts. in Santa Cruz and Cochise cos., Arizona, and the Mogollon Mts. in southern Catron Co., New Mexico, south through northeastern Sonora in the Sierra Madre Occidental to west-central Chihuahua. From elevations of ca. 1,500 m (Stone Cabin Canyon, Huachuca Mts., Santa Cruz Co., Arizona) to 2,600 m (summit of the José Mts., Sonora). Flowers mostly from July to October, but some populations in Mexico as early as May.

Representative specimens examined:

UNITED STATES. NEW MEXICO: Catron Co.: On or near the West Fork of the Gila R., Mogollon Mts., *Metcalfe 555* (ARIZ, GH, MO, NMC, US). ARIZONA: Cochise Co.: Huachuca Mts., *Harrison & Kearney 5773* (US). Fort Huachuca, *Wilcox in 1892* (NY). Near Fort Huachuca, *Wilcox 253* (US). Huachuca Mts., 7000 ft, *Jones in 1903* (DS, POM, US). Huachuca Mts., *Toumey in 1894* (GH, RM, US). Tanner's Canyon, Huachuca Mts., *Gilbert in 1892* (NY). Tanner's Canyon, Huachuca Mts., *Lemmon in 1882* (UC). Ramsey's Canyon, Huachuca Mts., *Goodding 786* (RM, US). Miller Canyon, Huachuca Mts., *Carter in 1936* (NMC). Carr Peak, Huachuca Mts., 6500 ft, *Benson 10500* (POM). Carr Peak, Huachuca Mts., *Goodding 222* (ARIZ, GH, NEB, NY, OKLA, RM). 5.6 mi up Carr Canyon road from Arizona 92, Huachuca Mts., *Towner 106* (DS). Reef Mine, Huachuca Mts., 7100 ft, *Gould*

1475 (ARIZ, UC). Garden Canyon, Huachuca Mts., *Harrison & Kearney 5773* (ARIZ). Near Fort Huachuca, Huachuca Mts., *Lemmon 2700* (GH). Rucker Canyon, upper left fork, Chiricahua Mts., *Blumer 2025* (F). Sugar Loaf Mt., Chiricahua Mts., *Darrow in 1937* (ARIZ). N slope of Sugar Loaf, Chiricahua National Monument, *Clark 8280* (ARIZ). Sugarloaf Trail just below tunnel, Chiricahua National Monument, *Towner 107* (DS). Near summit of pass, Chiricahua Mts., *Goodding 165-47* (ARIZ). Pine Canyon, Chiricahua Mts., 6700 ft, *Blumer 1610* (ARIZ, DS, F, MO, NEB, NMC, NY, RM, US). Ida Peak, along Telephone Trail, Chiricahua Mts., 8,000 ft, *Stone 517* (PH, RM). Pinery Canyon, Chiricahua Mts., 7,000 ft, *Barr 64-353* (ARIZ). 12.4 mi W of jct. of Arizona 186 & 181, in Pinery Canyon, Chiricahua Mts., ca. 7,000 ft, *Towner 164* (DS). 12.5 mi W of jct. Arizona 186 & 181, *Towner 171*. 1 mi below Onion Saddle, E. side of Chiricahua Mts., *Kaiser 49-209* (ARIZ). Crest Trail, Chiricahua Mts., 7,000 ft, *Hernbrode 136* (ARIZ). Gut Saw Canyon, Chiricahua Mts., *Goodding 2339* (UC). Wonderland of Rocks, Chiricahua Mts., *Darrow in 1937* (GH, NY). Bonita Canyon, Chiricahua Mts., *Henderson in 1933* (TEX). Outlaw Canyon, Chiricahua Mts., *Goodding 2339* (RM). Pima Co. (?): Sabino Canyon, Catalina Mts., 3,000 ft, *Jones in 1903* (MO, specimen immature; either not of this species or locality incorrect). Santa Cruz Co.: Madera Canyon, Santa Rita Mts., 5,900 ft, *Darrow 2614* (ARIZ). Madera Canyon, Santa Rita Mts., *Peebles et al. 4545* (ARIZ, US). Stone Cabin Canyon, Santa Rita Mts., 5,000 ft, *Thornber in 1903* (ARIZ). Santa Rita Mts., 6,000–8,000 ft, *Pringle in 1881* (F, GH). Santa Rita Mts., 7,000 ft, *Darrow & Arnold in 1936* (MO, OKL). Upper Madera Canyon, Santa Rita Mts., *Clark 12351* (GH, OKL). Along trail from Mount Wrightson to White House Canyon, Santa Rita Mts., 7,000 ft, *Parker et al. 5835* (ARIZ, NY).

MEXICO. SONORA: Puerto de los Aserrados, region of the Río de Bavispe, *White 3190* (ARIZ). Summit of the José Mts., 8,600 ft, *Mearns 1606* (DS, US). Cananea, *Murdoch in 1914* (F). CHIHUAHUA: 48 mi W of Matachic on road to Ocampo, 8,400 ft, *Wiens 3445* (COLO, DS). Mojarachic (Maguarachic?), *Knobloch 5094* (F). Mts. NW of Chihuahua, *Le Sueur in 1936* (MO, TEX, UC, US). San José de Pinal, Río Mayo, 7,000 ft, *Gentry 2587* (ARIZ, F, MO, POM, UC, US). Mts. SW of Chuchuichupa, *Hartman 712* (F, NY, UC, US). Mexican NW railroad, km 85, *Barlow in 1911* (F). Ridge between Río Chico and Río Caballo, Mexican NW railroad, Continental Divide, *Barlow in 1911* (F). Carretas, *White 993* (ARIZ). 130 mi W of Chihuahua City, 8,500 ft, *Russell in 1957* (UC). Cañon Huahuatán, 10 mi SE of Madera, *Muller 3428* (UC). Guayanopa Canyon, Sierra Madre, *Jones in 1903* (POM). Salto de Babicora, *Le Sueur 1407* (F). W from Pearson (now Juan Mata Ortíz), Sierra Madre, *Barlow in 1911* (F). Sierra Madre, *Nelson 6088* (US). No specific locality, *Le Sueur 101* (F, TEX).

This most distinct of the large-flowered members of sect. *Salpingia* is readily separated using any of several characters, including its exclusively montane distribution, fascicles of large axillary leaves, tall erect stems, long sepal tips, partially dehiscent capsule, and unusual ultraviolet absorption pattern on the petals. Apparently completely allopatric to the other taxa of sect. *Salpingia*, *Calylophus toumeyi* experiences no current genetic exchange with them. The absence of any intermediate collections and the number of characters which show discontinuities from *C. hartwegii* indicate the validity of specific status for *C. toumeyi*, which was not recognized in an earlier publication (Towner & Raven, 1970).

Distributed in the mountains of southeastern Arizona, southwestern New Mexico, and northeastern Mexico, this species is physically and ecologically separated from other members of sect. *Salpingia*. The blooming period is unusual for the genus, occurring in late summer and early fall in response to summer rainfall. Earlier flowering is prevented by the late, dry spring, characteristic of montane areas in this region.

Flower visitation to *C. toumeyi* seems sporadic, as insects were seen only once in significant numbers during several attempted studies. On that occasion, in the Chiricahua Mts., of Arizona (*Towner 238*), bees of the genus *Lasioglossum* were active gathering pollen shortly before dusk, and again after sunrise. Hawk-

moths were abundant visitors in the evening. Morphological characters and anthesis times suggest that hawkmoths are the principal pollen vectors. The floral tube attains a length of 70 mm in some specimens, the maximum seen in *Calylophus*, and is perhaps a response to pollination by the genera of sphingids with longer tongues (cf. Gregory, 1964). Moderately absorptive to ultraviolet light over their entire area, the petals have no contrast pattern, nor do they contrast with vegetative parts (Fig. 12). Anthesis occurs ½ to 1½ hours before sunset. Bees are therefore not likely to be regular and significant contributors to pollination.

Self-incompatibility is probably typical for this species. Only one plant was checked by self-pollination, and it was self-sterile. In one field study, a population was observed to have set no seed in spite of having been in flower for several weeks. The same population showed over 60% fertile capsules on the date of the cited pollination study.

Three plants from two Arizona populations were examined cytologically and proved to be heterozygous for two translocations apiece. Multivalent associations included a ring of 6 chromosomes in 1 plant and 2 rings of 4 chromosomes in the 2 others. One of each type of configuration was found in a population from the Chiricahua Mountains (*Towner 107*), indicating that at least 3 translocation polymorphisms were present in the population. Chromosome determinations from hybrids were not obtained because of the difficulty of crossing *C. toumeyi* and *C. hartwegii* and because of the scarcity of floral buds on those hybrids which were produced.

4. **Calylophus tubicula** (A. Gray) Raven, Brittonia 16: 286. 1964.

Oenothera tubicula A. Gray, Pl. Wright. 1: 71. 1852.

Herbaceous or slightly suffrutescent short-lived perennial, arising from a slender woody caudex; stems one to several, sparingly branched above, subdecumbent-ascending to nearly erect, 0.4–5.3 dm high; plant with short glandular pubescence throughout, or with some parts minutely strigulose. Leaves ± dense, subsessile, ascending, linear to ovate or obovate, 7–46 mm long, 0.7–11 mm wide, the tip acute, sometimes obtuse in lowermost leaves, the base acute-attenuate, the margin entire or sparsely and shallowly serrulate, occasionally slightly undulate; fascicles of small leaves 2–15 mm long in nonfloriferous axils; lowest stem leaves more frequently oblanceolate than above. Inflorescence dense, with buds crowded near the stem apex; buds terete. Floral tube funnelform in upper one-half or more, often tubular below, 5–25(–33) mm long, 3–10 mm wide at the throat in pressed specimens, the inner surface glabrous above to densely pubescent basally, yellow, sometimes fading pink, and more rarely, purplish. Sepals 3–13 mm long, 2–6 mm wide, with subulate free tips 0.5–2 mm long, plane, yellow, rarely with purple marginal stripes, only infrequently fading pink or purplish. Petals suborbicular to obovate-truncate, 5–20(–25) mm long, similar in width, infrequently fading pink to purplish, highly ultraviolet-reflective, with a large basal ultraviolet-absorptive spot. Stamens subequal; filaments 1–6 mm long, glabrous to minutely pubescent; anthers 2–7 mm long, sparsely and minutely

pubescent. Style 9–30(–40) mm long, usually exceeding the stamens, glabrous above, minutely pubescent below; stigma discoid to squarish, 1–2.5 mm broad; ovary 4–11 mm long, 0.5–1.5 mm wide. Capsule 8–19 mm long, 1.5–2.5 mm wide, moderately thin walled, completely dehiscent; seeds 1.0–1.4 mm long, obovoid, angled, truncate at the apex. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. TEXAS: prairies beyond the Pecos River, probably in eastern Pecos Co., August 1849, *Charles Wright 197* (in part = *821*; GH).

Distribution (Fig. 17): Primarily on limestone soils in arid lowlands, but occasionally in montane areas, from Guadalupe Co., New Mexico, south to western Texas, thence northeast to Howard Co., Texas and south to northern Zacatecas, south-central Nuevo León, and southwestern Tamaulipas. From ca. 600–1,800 m elevation. Flowers April to August.

Cytological relationships, interfertility, and a number of morphological characters demonstrate a close affinity between *Calylophus tubicula* and the other members of sect. *Salpingia*. However, the short-tubed, funnelform flowers (Fig. 4) and morning anthesis of this species constitute a phenetic similarity to sect. *Calylophus*, a relationship likely due to evolutionary convergence. *Calylophus tubicula* is distinguished from its closest relatives by those same characters. In addition, individuals of this species are shorter-lived than in other forms in the section. The plants rarely have large taproots, and are difficult to maintain for more than one or two years in cultivation.

Self-sterility was found in six plants from two populations of *C. tubicula* subsp. *tubicula*, and no evidence of self-compatibility was seen in any cultivated or wild plants of either subspecies. Stigmas were invariably well exserted and no greenhouse specimens of either subspecies ever set seed spontaneously. Anthesis occurred just before dawn (½ to 1½ hours before sunrise) at two colonies of *C. tubicula* subsp. *tubicula* in Eddy Co., New Mexico and in cultivated representatives of both subspecies. Stamens, the stigma, and a large spot at the base of each petal are ultraviolet-absorptive, contrasting markedly with the rest of the petal surface, which is highly reflective.

Flower visitors at field sites (*Towner 14, 15*) of *C. tubicula* subsp. *tubicula* consisted primarily of small halictid bees of several genera, especially *Evylaeus*, *Dialictus*, and *Agapostemon*. These were most active from just before sunrise to mid-morning, gathering both pollen and nectar. Infrequent visits by hawkmoths (*Hyles lineata*) were observed shortly before sunrise. In some colonies, removal of pollen was virtually complete by afternoon. Field data, anthesis times, and flower morphology indicate that this species is predominantly bee-pollinated. A strong inference can be made that *C. tubicula* evolved from a moth-pollinated ancestor resembling *C. hartwegii*. This is based on the relatively long floral tubes in some *C. tubicula* and on the close phenetic and cytogenetic relationship of the two species.

Relative to other forms of *Calylophus*, *C. tubicula* has a low level of chromosome heterozygosity. Eight of 14 plants examined had multivalents, and no evidence of inversions, diminutive chromosomes, or polyploidy was found. The

average number of observable translocation heterozygosities per plant was 0.7, as compared with 1.0 for the rest of sect. *Salpingia* and 1.9 for *C. berlandieri*.

Individuals from certain populations of *C. tubicula* may approach or exceed the minimum floral tube length seen in *C. hartwegii*. In such cases, *C. tubicula* generally retains the wider funnelform shape of the tube. Other populations show vegetative characteristics which suggest recent introgression with or derivation from *C. hartwegii*. These cases will be discussed under the subspecies.

Differences of pubescence, leaf shape, floral pigments, and ecological distribution distinguish the two subspecies listed below. The extremes of each form are quite distinct, but individuals from several collections in Mexico cannot be assigned with certainty to either taxon.

KEY TO SUBSPECIES

a. Glandular-pubescent throughout; leaves narrowly lanceolate to ovate; flowers rarely fading reddish or purple .... 4a. subsp. *tubicula*

aa. Minutely grey-strigulose on the ovary and upper stems; leaves linear to narrowly lanceolate; flowers commonly fading reddish or purple .... 4b. subsp. *strigulosus*

4a. **Calylophus tubicula** (A. Gray) Raven subsp. **tubicula**.—FIG. 4.

Galpinsia tubicula (A. Gray) Small, Bull. Torrey Bot. Club 23: 186. 1896. *Oenothera hartwegi* Benth. var. *tubicula* (A. Gray) H. Lév., Monogr. Onoth. 335. 1908.

Oenothera tubicula A. Gray var. *demissa* A. Gray, Pl. Wright. 1: 71. 1852. TYPE: United States, Texas, Culberson Co., on the Guadalupe Mts., October 1849, *Charles Wright 197*, in part = *13380* (GH, holotype; US, isotype). The collection probably came from Texas and not New Mexico (McKelvey, 1955: 1070).

Oenothera × *serrulatoides* H. Lév., Monogr. Onoth. 335. 1908. TYPE: United States, Texas, Pecos Co., valley of the Pecos and towards the Limpio, June 1851, *Charles Wright 1077* (MO, holotype; GH, NY, PH, isotypes). Remark on type sheet: "mais hybride de tubicula × serrulata?"

Galpinsia glandulifera A. Nels., Amer. J. Bot. 21: 575. 1934. TYPE: United States, New Mexico, Eddy Co., sandy hillsides, vicinity of Carlsbad Caverns, May 1930, *Gladys Convis 36* (RM). Published erroneously as *37*.

Galpinsia carlsbadiana A. Nels., Amer. J. Bot. 23: 269. 1936. TYPE: United States, New Mexico, Eddy Co., near the Caverns, Carlsbad National Park, 24 May 1931, *Aven Nelson 11396* (RM, holotype; DS, NY, POM, isotypes).

With short glandular pubescence throughout. Leaves narrowly lanceolate to ovate or obovate, 7–46 mm long, 0.7–11 mm wide, usually entire or nearly so. Flowers rarely fading reddish or purplish upon wilting. Self-incompatible. Gametic chromosome number, $n = 7$.

Distribution (Fig. 17): Colonial, primarily on limestone soils, in flat arid grasslands, often with *Larrea divaricata* and *Yucca*, from Guadalupe Co., New Mexico, south in the western side of the Pecos River drainage to western Texas, where occurring from Culberson Co. east to Howard Co., thence south through Presidio, Brewster, and Terrell cos., and probably most of central Coahuila, to northern Zacatecas, southwestern Nuevo León, and southwestern Tamaulipas. Elevational distribution from ca. 600 m (10 mi E of Dryden, Terrell Co., Texas) to ca. 1,400 m (between Santa Rosa and Vaughn, Guadalupe Co., New Mexico). Flowers April to August.

Representative specimens examined:

UNITED STATES. NEW MEXICO: Chaves Co.: Ca. 4 mi N of Roswell, *Towner 127* (DS). Eddy Co.: 4 mi W of Hope, *Munz & Gregory 23350* (RSA). Memorial Hospital, N end of Carlsbad, *Munz & Gregory 23353, 23354, 23356* (RSA, UC). 0.6 mi W of Hope, *Towner 14* (DS). 1.7 mi NE of Hope, *Towner 16* (DS). Ca. 4.5 mi S of Carlsbad, *Towner 17* (progeny only, DS). 7.6 mi NE of White's City, *Towner 18* (DS). Otero Co.: Ca. 5 mi W of Elk (1 plant), *Towner 108* (DS). TEXAS: Brewster Co.: 41 mi S of Alpine, *Anderson 3030* (DS). Flats near Old Blue, Glass Mts., *Warnock W524* (DS, POM, TEX). 15 mi E of Marathon, *Munz & Gregory 23400* (RSA, UC). Ca. 10 mi E of Alpine, *Sperry T1095* (UC, US). 6 mi S of Marathon, *Rollins & Chambers 2766* (DS, GH, POM, RM, UC). Culberson Co.: 3 mi SW of New Mexico line on U.S. 180, *Munz & Gregory 23360* (RSA). 9 mi E of Van Horn, *Waterfall 4162* (ARIZ, GH, MO, NY). Ector Co.: W of Odessa, *Lundell & Lundell 16921* (LL). Jeff Davis Co.: 8 mi S of Fort Stockton, *Munz & Gregory 22385* (RSA, UC). Pecos Co.: "Mesa slope," *Tharp 43-731* (OKL, OKLA, RM, TEX, CC). Ca. 20 mi W of Sanderson, *Warnock & McBryde 14904* (LL, TEX). 11 mi E of Fort Stockton, *Warnock 5164* (LL, SMU). 30 mi NE of Fort Stockton, *Ownbey & Ownbey 1625* (MO, POM, RM, RSA, UC). Presidio Co.: Up to divide between Long Draw and Capote Draw on road from Marfa to Ruidosa, *Hinckley* (NY, SMU). Cleveland Ranch, near Chinati Mts., *Hinckley* (GH, NY). 5 mi N of Marfa, *Munz & Gregory 23389* (RSA, UC). Reeves Co.: On U.S. 80, 3 mi E of intersection with U.S. 290, *Munz & Gregory 23370, 23371, 23372* (RSA, UC, WTU). On U.S. 80, 1 mi E of intersection with U.S. 290, N edge of the Davis Mts., *Waterfall in 1943* (GH, MO, NY). Plains W of Pecos, *Tracy & Earle 144* (F, GH, MO, NEB, NY, TEX). Terrell Co.: 10 mi E of Dryden, *Parks et al. 56* (TEX). Upton Co.: 20 mi SE of Crane, *Raven & Gregory 19240*. Val Verde Co.: Pumpville, *Fisher 290* (US). Ward Co.: N of Pyote, *Lundell & Lundell 11379* (POM, SMU).

MEXICO. ZACATECAS: 18 km W of Concepción del Oro, *Stanford et al. 590* (DS, MO, NY). SAN LUIS POTOSÍ(?): "Prov. de San Luis," *Octoust 1050* (P).

This subspecies occurs primarily on arid calcareous flats and outcrops in southeastern New Mexico and western Texas. Its distribution in northern Mexico is very poorly known, and may include much of Coahuila in addition to the localities listed. In southern New Mexico, it occurs in the Pecos River Valley and on the plains to the west of it. Other taxa of *Calylophus* supplant *C. tubicula* on the higher plains to the east of the river (the "Llano Estacado").

The broader leaves and glandular pubescence are the primary characters differentiating *C. tubicula* subspp. *tubicula* and *strigulosus* from one another. Introgression between the two seems to occur in Nuevo León, Tamaulipas, and Coahuila. Intermediate specimens are cited under subsp. *strigulosus*.

Twelve plants from 9 populations have been examined during meiosis; 6 had 5 bivalents and a ring of 4 apiece, while 6 had 7 bivalents. Experimental hybrids were obtained with difficulty between *C. tubicula* subsp. *tubicula* and *C. berlandieri* subsp. *berlandieri*. These plants were weak and essentially sterile (0–1% pollen fertility). They showed low chiasma frequency and gave evidence of at least 6 major translocation differences between the forms. Crosses of *C. tubicula* subsp. *tubicula* with other members of sect. *Salpingia* produced progeny which were structurally homozygous or heterozygous for 1 or 2 translocations. Such crosses produced good seed set and reasonably fertile hybrids, although the hybrids frequently showed poor germination and viability.

Introgression between this subspecies and *C. hartwegii* subsp. *fendleri* has been imputed by Munz (1965). Actually, considerable differences in elevational distribution separate *C. hartwegii* subsp. *fendleri* and *C. tubicula* subsp. *tubicula*, the former occurring from ca. 1,500 to 2,150 m elevation in New Mexico. This should make contact between these taxa infrequent. In the Carlsbad Caverns

area, individuals with broad leaves and long floral tubes have been treated as a distinct taxon, *Galpinsia carlsbadiana*, and as possible hybrids between the forms mentioned above. The latter possibility seems remote, since I have discovered no records of *C. hartwegii* subsp. *fendleri* within 160 km of the Caverns area. Taxonomic recognition is unwarranted also for the reason that the long-tubed forms occur together with typical *C. tubicula* in many populations throughout the range of subsp. *tubicula*. It is uncertain whether this pattern should be interpreted as a result of present or past genetic exchange or as spontaneous variation within *C. tubicula*. Collections of *C. tubicula* subsp. *tubicula* showing long floral tubes include the following: 4 mi N of Carlsbad Caverns, Eddy Co., New Mexico, *Porter & Porter 8986* (DS, RM; of all collections, this is the most hybrid-like, being very similar to *C. hartwegii* subsp. *fendleri*). 45 mi S of Pecos, Pecos Co., Texas, *Moore & Moore 21* (NY, SMU, UC). 1–5 mi NW of Notrees, Ector Co., Texas, *Collins 82* (OKLA). Borrow pits N of Pecos, Reeves Co., Texas, *Nelson & Nelson 4989* (DS, MO, RM, TEX, UC, US).

In general, *C. tubicula* subsp. *tubicula* was not found growing together with other forms of *Calylophus*, perhaps because of its restriction to xeric sites at low elevations. In Chaves Co., New Mexico, two individuals of *C. hartwegii* subsp. *pubescens* (*Towner 126*) were found in a large population of *C. tubicula* (*Towner 127*), but with no evidence of hybrids. Likewise, no hybrids were apparent in a situation near the Glass Mountains in Brewster Co., Texas, where *C. tubicula*, *C. lavandulifolius*, and *C. hartwegii* subsp. *pubescens* were all discovered within a 0.3 mile stretch of graded roadside. To the north of Roswell, New Mexico, *C. tubicula* was observed growing within a few miles of *C. hartwegii* subsp. *filifolius* in apparently identical habitats. It can be inferred that these two taxa occasionally come into contact. Their similarity in pubescence might well be a result of some past genetic exchange, although I have seen no signs of current hybridization.

4b. **Calylophus tubicula** subsp. **strigulosus** Towner, subsp. nov.

Differt a subsp. *tubicula* ovario et caulibus superis minute strigulosis, foliis linearibus vel anguste lanceolatis, et floribus plerumque rubescentibus vel purpurascentibus.

Minutely grayish-strigulose on the ovary and upper stems, sometimes throughout, glandular pubescence generally absent. Leaves linear to narrowly lanceolate, 10–35 mm long, 0.8–3 mm wide, often shallowly serrulate. Flowers commonly fading reddish to purple. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: MEXICO. NUEVO LEÓN: Along Highway 60, 2 mi W of Galeana Jct., dry rocky open range, 1,700 m, 5 July 1963, *McGregor, Harms, Robinson, del Rosario, & Segal 119* (DS-504949, holotype; KANU, SMU, isotypes).

Distribution (Fig. 17): Uncommon in rocky open sites and canyons in relatively dry montane areas, sometimes in pine forest; southernmost Coahuila, south-central Nuevo León, and southeastern Tamaulipas. From ca. 1,500 to 2,300 m elevation. Records of flowering include July and August.

Representative specimens examined:
MEXICO. NUEVO LEÓN: 15 mi SW of Galeana, *Mueller & Mueller 464* (F, TEX). Hacienda

Pablillo, Galeana, *Taylor 68* (ARIZ, DS, MO, NY, TEX, UC). On canyon wall, 5,400 ft, municipality of Galeana, *Chase 7745* (ARIZ, F, MO, NY). Ca. 35 mi S of Galeana towards Ascención, *Straw & Forman 1374* (RSA). Near summit of Nuevo León Highway 60 W of Galeana, *Sanderson 287, 288* in part (TEX). COAHUILA: SE of Saltillo, *Clark 6710* (MO). Fraile, 59 km S of Saltillo, *Stanford et al. 242* (DS, MO, NY, UC). TAMAULIPAS: 3 mi N of Miquihuana, *Stanford et al. 2472* (DS, NY, RSA, WTU). Jaumave Valley, *Nelson 4461* (US).

The ecological distribution of *Calylophus tubicula* subsp. *strigulosus*, which occurs in montane areas of northeastern Mexico, often with pines, contrasts sharply with that of subsp. *tubicula*. The feature in common between the two distributions is perhaps aridity, although the Mexican sites would appear to be more mesic.

Several collections assigned to this subspecies show similarity to subsp. *tubicula*. Typically such resemblance consists of combinations of strigulose and glandular pubesence or of glandular pubescence and leaves as found in subsp. *strigulosus*. Of the collections cited above, intermediacy is shown by *Clark 6710, Nelson 4461*, and *Stanford et al. 2472*. Populations in the area of the type locality seem the most distinct from subsp. *tubicula*.

Two plants cultivated from seed had 3 bivalents and 2 rings of 4 chromosomes at meiosis, each thus being heterozygous for 2 translocations. These specimens showed morning anthesis similar to that seen in subsp. *tubicula*. No field collections or observations were made.

Introgression between *C. hartwegii* subsp. *hartwegii* and *C. tubicula* in northern Mexico may have given *C. tubicula* subsp. *strigulosus* its distinguishing characteristics. Such hybrid origin may have occurred quite recently since the two forms still occur in close proximity and in similar habitats in the Sierra Madre Oriental. The strigulose pubescence, greater prominence of anthocyanins, and narrow leaves of subsp. *strigulosus* in comparison to subsp. *tubicula* all represent points of similarity to the local populations of *C. hartwegii* subsp. *hartwegii*. Of the few collections we have from this area, one set seems to be fully intermediate with *C. hartwegii*, having a floral tube length of 19–21 mm [15 mi SW of Galeana, Nuevo León, *Mueller & Mueller 464* (F, TEX)].

Section II. **Calylophus**.

Calylophus Spach, Hist. Nat. Vég. Phan. 4: 349. 1835. *Oenothera* subgen. *Calylophus* (Spach) Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840.

Meriolix Raf. ex Endl., Gen. Pl. 1190. June 1840; Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. 1819, nom. nud. Raf., J. Phys. Chim. Hist. Nat. Arts 89: 259. 1819, nom. nud.

Herbaceous to suffrutescent perennials or annuals, 1–8 dm high, glabrous to strigulose or strigulose-canescent. Leaves 1–9 cm long, subentire to spinuose-serrate. Inflorescence dense, with buds usually crowded at the stem apex; buds squarish in cross-section. Flowers opening near sunrise. Floral tube funnelform and somewhat squarish in cross-section distally, tubular in proximal one-third to one-half of length, 2–20 mm long. Sepals with keeled midribs. Petals suborbicular to obcordate. Stamens biseriate, the episepalous filaments about twice as long as the epipetalous filaments. Capsule often tardily dehiscent, sometimes slightly recurved.

TYPE SPECIES: *Calylophus serrulatus* (Nutt.) Raven.

5. **Calylophus berlandieri** Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 272. 1835.

Herbaceous to suffrutescent perennial or annual arising from a woody caudex; stems one to many, simple to moderately branched, subdecumbent to erect, 1–8 dm high, glabrous to strigulose or strigulose-canescent, especially above. Leaves sessile or indistinctly petiolate, sometimes early deciduous below, spreading to more or less ascending, linear to narrowly lanceolate or oblanceolate, often folded lengthwise, 1–9 cm long, 0.1–0.9 cm wide, usually not much reduced up the stem, the abaxial surface glabrous to strigulose-canescent, especially at the base, the adaxial surface glabrous to sparsely strigulose, the tip acute, the base attenuate, the margin subentire to spinuose-serrate; fascicles of small leaves to 20 mm long often present in nonfloriferous axils; lowest stem leaves narrowly oblanceolate to oblanceolate or even spatulate. Inflorescence more or less compact, with buds usually crowded at the stem apex and one to several flowers fresh at one time, sparsely and minutely strigulose to densely strigulose-canescent; buds squarish in cross-section. Floral tube funnelform and somewhat squarish in cross-section distally, tubular in proximal one-third to one-half of length, 5–20 mm long, 3–14 mm wide at the throat in pressed specimens, subglabrous to strigulose-canescent without, especially along the midribs, within glabrous distally and minutely pubescent to strigulose basally, pale yellow green, sometimes blue black within, rarely fading pinkish. Sepals 4–12 mm long, 2–7 mm wide, with subulate free tips 0–4 mm long, with raised or keeled midribs, subglabrous to strigulose-canescent, pale yellow green, occasionally with red midribs and tips, only rarely fading pinkish. Petals suborbicular to obovate-truncate or obcordate, 6–25 mm long, 7–30 mm wide, occasionally becoming orangish to purplish on wilting, highly ultraviolet-reflective, but with large basal ultraviolet-absorptive spot. Stamens biseriate; episepalous filaments 2–8 mm long, the epipetalous filaments 1–4 mm long; anthers 2–7 mm long; pollen fertility normally 85–100%. Style 9–30 mm long, glabrous above and glabrous to minutely pubescent basally; stigma discoid to squarish, 1–3 mm broad, sometimes blue black, generally exserted to the ends of the anthers or beyond; ovary 5–20(–27) mm long, 0.5–1.5 mm wide, minutely strigulose to strigulose-canescent. Capsule 10–35 mm long, 1–2 mm wide, hard and thick walled, completely and often tardily dehiscent, sometimes slightly recurved; seeds 1–1.8 mm long, sharply angled, truncate at the apex. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. TEXAS: on shore of Espiritu Santo Bay, probably in present Calhoun Co., March or May 1829, *Jean Louis Berlandier 539 = 1919* (P, holotype; GH, PH, isotypes). This locality is given on the Gray Herbarium sheet and by Spach (1835b: 338). The date was determined from information given by McKelvey (1955).

Distribution (Fig. 18): Open, moderately dry areas on a variety of well-drained soils, frequently calcareous, in southeastern Colorado, southwestern Kansas, western and central Oklahoma, eastern New Mexico, Texas (except in the northeast), Louisiana, north-central Coahuila, northern Nuevo León, and

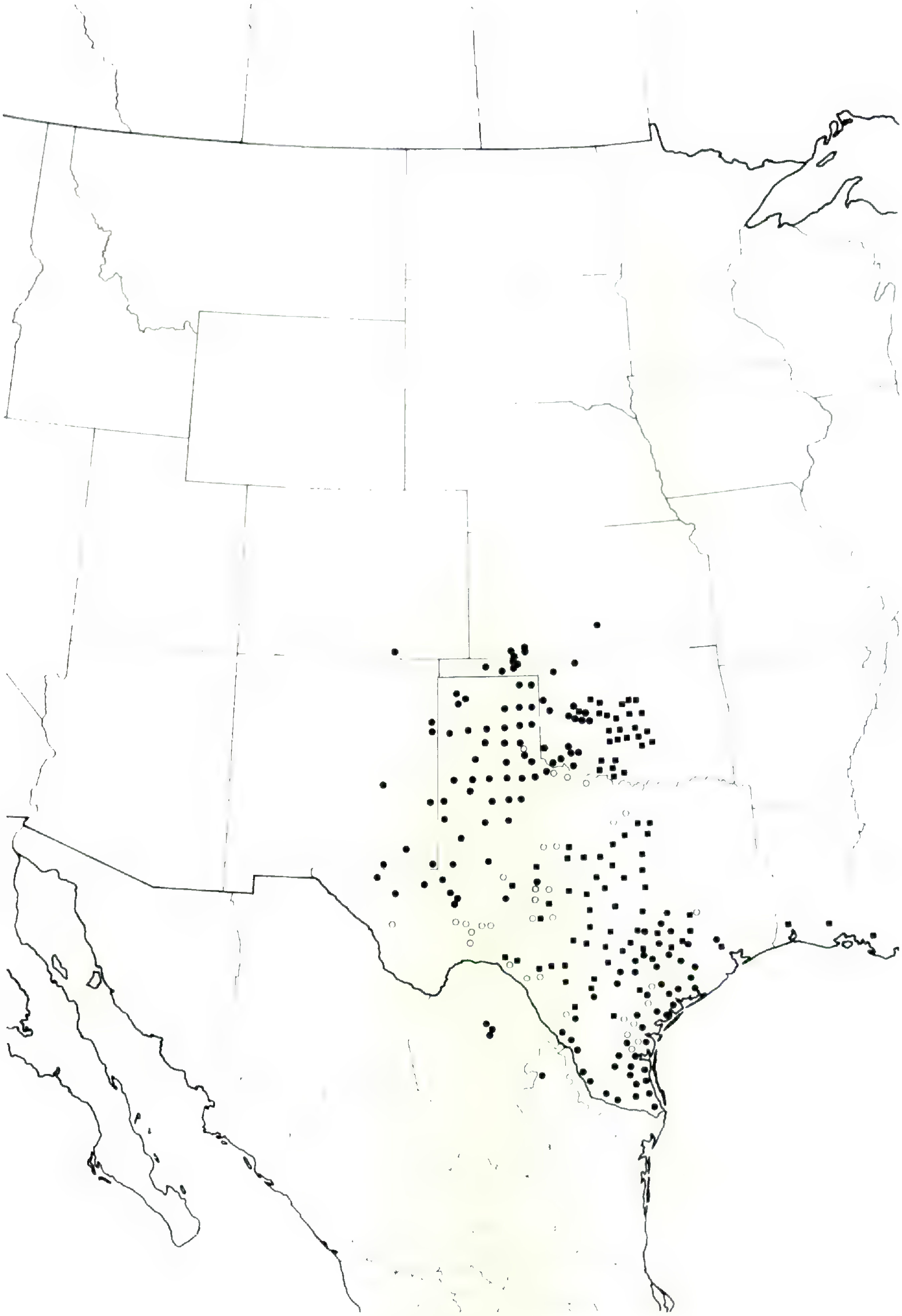


FIGURE 18. Distributions of *Calylophus berlandieri* subsp. *berlandieri* (dots), *C. berlandieri* subsp. *pinifolius* (squares), and intergrades between the two subspecies (open circles).

perhaps northern Tamaulipas. From sea level to ca. 1,200(–1,800) m elevation. Flowering March to September.

An outcrossing species, *Calylophus berlandieri* is characterized by self-incompatibility, large flowers, and the absence of permanent complex structural hybridity. Incompatibility systems of the S-allele type were demonstrated by Linder & Brun (1957) in plants of this species. I tested 24 plants from 6 populations and found all to be self-sterile. The yellow flowers are morning opening, open throated, and have petals with conspicuous contrast patterns in the long-wave ultraviolet region (Fig. 14). A variety of diurnal and matinal insects, including skippers, small butterflies, bees of various families, and beetles, were observed as flower visitors. These groups probably make varying contributions to pollination at different localities, but no highly specific relationship appears to have evolved with any particular type of insect.

Analysis of meiotic pairing in this species demonstrated a high frequency of translocation heterozygosity. Of 68 plants analyzed from 45 populations, 56 or fully 82% were heterozygous for 1 to 5 reciprocal translocations. The most frequent classes of chromosomal types were those with 1 or 2 interchanges, but several plants had as many as 5 translocation heterozygosities. No permanent structural hybridity was proven in this self-incompatible species, but the high frequency of heterozygotes implies that some developmental or selective effect probably reduced the numbers of homozygotes.

As reported by Towner & Raven (1970), Berlandier's type possesses highly fertile pollen, indicative of the pair-forming, outcrossing species in this group. A later examination of the pollen from isotypes of *C. drummondianus* revealed that those plants were only half-fertile. Further study of the specimens and their localities made it obvious that they were complex structural heterozygotes, thus belonging with *C. serrulatus.* This leaves *C. berlandieri* as the earliest available name for the outcrossing species.

The taxonomic separation of *C. berlandieri* from *C. serrulatus* on the basis of differences in cytology and breeding systems rationalized a formerly confusing situation in regard to geographical variation. As previously interpreted, these forms presented a complex pattern of countering trends in variation of floral and vegetative parts. In my treatment, there is less conflict in variation patterns, although the situation is still not simple. The two species exhibit parallel geographic variation, and both display a wide range of statures, leaf dimensions, and flower sizes. The parallelisms are seen primarily in vegetative characters, whereas the floral characters generally differ between the two species.

Calylophus berlandieri is polytypic, with two well-differentiated morphological races. *Calylophus berlandieri* subsp. *pinifolius*, a central Texas subspecies, intergrades with *C. berlandieri* subsp. *berlandieri* in southern and west-central Texas and, to a lesser extent, in the boundary between the Edwards Plateau and the coastal plain.

Populations of this species occasionally occur together with *C. tubicula*, *C. hartwegii*, and *C. lavandulifolius*, but I have seen no evidence of interbreeding. Numerous test crosses performed on those combinations only rarely produced

viable offspring, and these were completely pollen-sterile. Sympatric occurrences with *C. serrulatus* are infrequent, and will be discussed in the section on that species.

KEY TO SUBSPECIES

a. Stems several to many, subdecumbent to ascending, 1–4 dm tall; leaves 1–4 cm long .... 5a. subsp. *berlandieri*

aa. Stems one to several, suberect to erect, 3–8 dm tall; leaves 2.5–9 cm long .... 5b. subsp. *pinifolius*

5a. **Calylophus berlandieri** Spach subsp. **berlandieri**.

Oenothera berlandieri (Spach) Steud., Nom. Bot., ed. 2. 2: 206. 1841. *Meriolix berlandieri* (Spach) Walp., Repert. Bot. Syst. 2: 79. 1843. *Calylophus drummondianus* Spach subsp. *berlandieri* (Spach) Towner & Raven, Madroño 20: 243. 1970.

Oenothera serrulata Nutt. var. *typica* sensu Munz, Amer. J. Bot. 16: 712. 1929, pro parte. *Calylophus serrulatus* (Nutt.) Raven subsp. *serrulatus* sensu Shinners, Sida 1: 338. 1964, pro parte. *Oenothera serrulata* subsp. *serrulata* sensu Munz, N. Amer. Fl., ser. 2, 5: 141. 1965, pro parte.

Oenothera serrulata Nutt. var. *pinifolia* Engelm. ex A. Gray sensu Munz, Amer. J. Bot. 16: 715. 1929, pro parte. *O. serrulata* subsp. *pinifolia* (Engelm. ex A. Gray) Munz sensu Munz, N. Amer. Fl., ser. 2, 5: 141. 1965, pro parte.

Oeonothera serrulata Nutt. var. *drummondii* Torr. & A. Gray sensu Munz, Amer. J. Bot. 16: 714. 1929, pro parte. *O. serrulata* subsp. *drummondii* (Torr. & A. Gray) Munz sensu Munz, N. Amer. Fl., ser. 2, 5: 142. 1965, pro parte.

Perennial; stems several to many, moderately branched, subdecumbent to ascending, 1–4 dm high. Leaves more or less crowded, linear to narrowly lanceolate or oblanceolate, 1–4 cm long, 0.1–0.6 cm wide, the margin subentire to serrate, and occasionally somewhat undulate; lowest stem leaves frequently oblanceolate to spatulate. Sepals often with only slightly raised midribs, the free tips 0–2 mm long. Inside of floral tube and stigma yellowish, never black. Self-incompatible. Gametic chromosome number, $n = 7$.

Distribution (Fig. 18): Common on grassy prairies, plains, or low hills on sandy, gravelly, and limestone soils in relatively dry areas, frequently with *Prosopis*, *Quercus havardii*, and *Opuntia*, from western Las Animas Co., Colorado, Seward, Meade, and possibly Reno cos., Kansas, south through eastern New Mexico, the Texas Panhandle, and western Oklahoma to Culberson, Ward, and Crane cos., Texas, thence southeast near the Pecos and Rio Grande rivers to the Gulf Coast, becoming widespread on the Coastal Plain north to Milam Co., Texas; also occurring in the Santa Rosa Mts. of northern Coahuila and in northern Nuevo León. From sea level near the Texas coast to ca. 1,200 m (Rita Blanca Lake, Hartley Co., Texas), with one record at ca. 1,800 m elevation (12 mi S of Trinidad, Las Animas Co., Colorado). Flowers March to September.

Representative specimens examined:

UNITED STATES. COLORADO: Las Animas Co.: 12 mi S of Trinidad, *Brenckle 48184* (SMU). KANSAS: Meade Co.: Just S of spillway at Lake Larrabee, Meade Co. State Park, *Bare 24* (KANU). Reno Co.: Hutchinson, *Smyth 40* (US). Seward Co.: 14 mi NE of Liberal, *Stephens 11206* (KANU). NEW MEXICO: De Baca Co.: 35.5 mi S of Ft. Sumner, *Towner 130* (DS). Eddy Co.: 6 mi SW of White's City, *Munz & Gregory 23359* (UC, RSA). 11.4 mi SW of White's City, *Towner 21* (DS). Eddy or Lea Co.: Shinneries E of Carlsbad, *Goodding*

4586 (ARIZ). Lea Co.: S of Jal, *Barneby 14482* (DS). Quay Co.: Porter, *Suggs in 1942* (NMC). Roosevelt or Lea Co.: Between Tatum and Portales, *Goodding in 1937* (ARIZ). OKLAHOMA: Beaver Co.: 15 mi SW of Beaver City, *Stevens 366* (DS, NY, OKL, OKLA, SMU, US). Custer Co.: 1 mi S and 1 W of Weatherford, *Waterfall 1593* (ARIZ, NY). Harmon Co.: 1.1 mi W of Vinson, *Towner 87* (DS). Harper Co.: Supply, *Demaree 12392* (GH, OKL, POM, SMU). Jackson Co.: N bank of Red R., SW of Eldorado, *Towner 138* (DS). 8.8 mi W of Elmer, *Towner 139* (DS). Kiowa Co.: 17.8 mi N of Altus, *Towner 78* (DS). Roger Mills Co.: Antelope Hills, *Goodman 2618* (MO, NY, OKL, POM). Texas Co.: 11 mi E of Hardesty, *Stephens & Brooks 21758* (DS). Tillman Co.: 2.6 mi W of Tipton, *Towner 140* (DS). TEXAS: Aransas Co.: Aransas Bay, *Berlandier 567 = 1957* (GH, MO, POM, RSA). Armstrong Co.: 15 mi S of Claude (Palo Duro Canyon), *Stephens & Brooks 25469* (DS). Bailey Co.: 2 mi S of Muleshoe, *Ferris & Duncan 3397* (DS, MO, NY). Bastrop Co.: Bastrop Park, *Warnock 101* (TEX). Bexar Co.: 20 mi S San Antonio, *Metz 678* (NY, RM). Brooks Co.: 13.4 mi N of Hebbronville, *Towner 57* (DS). 14 mi S of Falfurrias, *Towner 60* (DS). 5 mi N of Falfurrias, *García 49* (OKLA, SMU, TEX). Caldwell Co.: W of Luling, *Crockett 218* (LL). Calhoun Co.: Port O'Connor, *Tharp in 1930* (TEX). 7.5 mi W and 5.6 mi N of Port O'Connor, *Towner 179* (DS). 2.4 mi E of Seadrift, *Towner 180* (DS). Callahan Co.: Ca. 17 mi SE of Abilene, *Henderson 64-52* (DS). Childress Co.: Estelline, *Reverchon 4307* (GH, MO, NY, POM, US). Concho Co.: 2.5 mi W of Eden, *Munz & Gregory 23426* (RSA). Crockett Co.: 25 mi W of Ozona, *McVaugh 8209* (LL, TEX). Dickens Co.: On side of canyon, S of U.S. 82, *Lundell 12979* (LL, TEX, US). Donley Co.: Jericho, *Demaree 12439* (DS, NY, OKL, PH, POM, TEX). Duval Co.: 15 mi E of Hebbronville, *Sandoval & McCart 7982* (OKLA, TEX). Gaines Co.: 3 mi S of Seagraves, *Tharp in 1941* (GH, SMU, TEX). Garza Co.: 2.5 mi E of Post, *Raven & Gregory 19304* (DS). Glasscock Co.: 3 mi E of Garden City, *Munz & Gregory 23422* (RSA, UC). Goliad Co.: Near Goliad, *Williams 9* (F, PH). Harris Co.: Spring, *Gentry 865* (RM). Hartley Co.: 10.4 mi N of Channing, *Roberts 35* (DS). Hemphill Co.: 7 mi ENE of Canadian, *Delso 122* (DS). Hidalgo Co.: 25 mi N of Edinburg, *Clover 811* (NY). Hutchinson Co.: Near Stinnett, *McFarland 13* (OKL, RM). Irion Co.: Barnhart, *Warnock T343* (TEX, US). Jackson Co.: 13.4 mi W Palacios, *Towner 176* (DS). Jim Hogg Co.: 9.7 mi E of Hebbronville, *Towner 56* (DS). Jim Wells Co.: 20 mi N of Premont, *Cabrera 102* (TEX). Kenedy Co.: El Toro I., *Tharp 49123* (in part, possibly a mixture with *C. serrulatus*; F, MO, OKLA, PH, POM, TEX, UC, US). 7.5 mi S of Riviera, *Towner 186* (DS). 17.8 mi N of Raymondville, *Towner 192* (DS). Kleberg Co.: 0.8 mi W of Riviera, *Towner 185* (DS). Kinney Co.: 9 mi W of Brackettville, *McVaugh 7685* (DS, F, SMU, TEX). La Salle Co.: Near Cotulla, *Small & Wherry 11941* (NY). Lee Co.: Giddings, *Hall 209* (F, GH, MO, NY, POM, US). Lipscomb Co.: 23.7 mi N of Canadian, *Rowell 10414* (DS). Live Oak Co.: Mikeska, *Owens & Parks 2407* (MO). Loving Co.: Between Mentone and Wink, *Warnock in 1952* (LL, SMU). Lubbock Co.: N of Lubbock, *Demaree 7528A* (DS, RSA, SMU, TEX). Motley Co.: 5.2 mi WSW of Matador, *Shinners 18668* (OKLA, SMU). Nueces Co.: Bishop, *Eifrig in 1926* (POM). Ochiltree Co.: 11.1 mi SE of Perryton, *Towner 158* (DS). Palo Pinto Co.: 19 mi W of Mineral Wells, *Warren 24* (DS). Pecos Co.: 30 mi W of Sheffield, *Munz 13290* (DS, POM, UC). Potter Co.: 1 mi N of Canadian R. on Highway 287, *Jefferson & Jefferson 2676* (DS, F, MO, NEB, NY, RM, SMU, UC, US, WTU). 11.3 mi N and 2.0 mi W of Amarillo, *Towner 91* (DS). Randall Co.: Palo Duro State Park, *Cory 13036* (LL, SMU). Refugio Co.: 8.9 mi W of Refugio, *McCart 6831* (SMU). San Patricio Co.: Near Mathis, *McKelvey 1726* (GH). Taylor Co.: 3 mi S of Camp Barkeley, *Tolstead 7096, 41983* (MO, NEB, NY, POM, SMU, UC). Terrell Co.: 13 mi S of Sheffield, *Webster 130* (TEX). Tom Green Co.: 7⅔ mi S of Christoval, *Cory 50569* (NY, SMU). Travis Co.: Austin, *Tharp in 1938* (SMU, UC). Uvalde Co.: 6 mi SE of Uvalde, *Munz 13316* (POM). Val Verde Co.: Ca. 1.9 mi from Del Rio, *Traverse 2162* (SMU, TEX). Victoria Co.: Inez, *Palmer 9137* (DS, US). Ward Co.: 3 mi ENE of Monahans, *McVaugh 8186* (DS, GH, LL, TEX). Webb Co.: 7 mi N of Laredo, *Dickey 129* (SMU, TEX). Wheeler Co.: 11.5 mi E of Shamrock, *Rowell 10080* (DS, RSA). Wilbarger Co.: 20 mi N of Vernon, *Towner 77* (DS). Willacy Co.: 1¼ mi from shore at Port Mansfield, *Webster & Wilbur 3074* (SMU, US). Wilson Co.: 5 mi N of Stockdale, *Munz & Gregory 23443* (RSA, UC). Winkler Co.: 11 mi W of Kermit, *Raven & Gregory 19228* (DS). Wise Co.: 3 mi N of Bridgeport, *Whitehouse 15278a* (SMU). Yoakum Co.: 4.7 mi N of Bronco, *Towner 135* (DS). Zapata Co.: 5 mi SE of San Ygnacio, *Flores & Flores 147* (TEX). Counties not known: From Bejar (San Antonio) to Austin, *Berlandier 479 = 1829* (GH). From Matamoros to Goliad, *Berlandier 1048 = 2478* (GH, MO, PH).

MEXICO. COAHUILA: Santa Rosa Mts., *Marsh 1354* (F, OKLA, SMU, TEX). Múzquiz, *Marsh 110* (F, OKLA, TEX). Hacienda Mariposa, Mcpo. of Múzquiz, *Wynd & Mueller 264* (ARIZ, MO, NY, US). Summit of La Cuesta Maleña Mts., *Reveal et al. 2594* (DS). NUEVO LEÓN: Lampazos, *Edwards 356* (F).

This relatively short-leaved and low-statured subspecies occurs over an extensive range on the plains of Texas and adjacent states. It is common in the Texas Panhandle and along the Gulf Coast, and it is also found locally in sandy areas of West Texas. As I have defined it, *Calylophus berlandieri* subsp. *berlandieri* incorporates elements from each of the three subspecies of "*Oenothera serrulata*" recognized by Munz (1965: 141–142).

For instance, the extremely narrow-leaved plants formerly known as *Oenothera serrulata* subsp. *pinifolia* are clearly variants which can actually be found along with broader-leaved plants in populations of either subspecies of *C. berlandieri.* My treatment of these forms is similar to that of Shinners (1964), who did not recognize subsp. *pinifolia*, viewing it as merely the extreme in a wide range of variation, the latter due to "spontaneous mutation." The narrow-leaved plants are most frequently found in areas of highly calcareous soil, including gypsum, and they occur in the more arid portions of the range of *C. berlandieri.* Thus their presence may well be due not to "spontaneous mutations," but to edaphic selection factors.

In the past, narrow-leaved individuals of *C. berlandieri* subsp. *berlandieri* were often assigned to *Oenothera serrulata* var. *pinifolia.* Examples are the following: 5 mi N of Stockdale, Wilson Co., Texas, *Munz & Gregory 23443* (UC, RSA). 2 mi S of Muleshoe, Bailey Co., Texas, *Ferris & Duncan 3397* (DS, MO, NY). Narrow-leaved individuals are slightly more frequent in *C. berlandieri* subsp. *pinifolius*, although they are not representative of that taxon as a whole.

The distribution of *C. berlandieri* subsp. *berlandieri* is divided into a Coastal Plains section and a Central Plains section. These two series of populations are connected only tenuously, this through a narrow zone along the Rio Grande southwest of the Edwards Plateau. The coastal region is less severe in climate than is the central region, but both areas are semiarid. Considering the breadth of these separate ranges, their distinctness, and their climatic differences, one might expect the two series of populations to have diverged morphologically. However, this does not appear to have been the case, as they show completely overlapping ranges of variation in all characters which I have examined.

In spite of the morphological similarity of the two series, meiotic pairing in hybrids suggests that considerable cytological divergence may have taken place. Nine hybrids between progeny of *Rowell 10414* (Lipscomb Co., Texas) and progeny of *Bohart & Thorp 650928-1* (Victoria Co., Texas) showed I_2/KI pollen stainability of approximately 40%. Meiotic determinations of 2 of the hybrids showed chains of 14 chromosomes, indicating the presence of at least 6 reciprocal translocation differences between the parents. Similar data were obtained from crosses of Rowell's collection with *Towner 185* (Kleberg Co., Texas).

The frequency of translocation heterozygosity in natural populations of *Calylophus berlandieri* subsp. *berlandieri* was found to be extremely high. Of 38

plants examined, including some grown from field-collected seed, only 6 formed 7 bivalents at meiotic metaphase. The remaining 84% showed multivalent formation in various degrees, indicating structural heterozygosity. The average number of translocations per plant was 2.0.

Flower visitation was observed at one site in Potter Co., Texas (*Towner 91*). Anthesis occurred shortly before sunrise, at which time several hawkmoths (*Hyles lineata*) visited flowers for nectar. At sunrise and afterwards, skippers, small butterflies, and bees of small to medium size, e.g., *Evylaeus* and *Agapostemon*, collected nectar and pollen from the flowers. Pollination was perhaps most effective with the anthophorid bees (*Melissodes* and *Anthophora*), which were few in number, however. Oligolectic halictids probably made some contribution, since they were common and because their appearance coincided closely with anthesis times.

Intergradation occurs between *C. berlandieri* subspp. *berlandieri* and *pinifolius* in several areas. Along the eastern escarpment of the Edwards Plateau, few natural intermediates are found, apparently because the respective habitats of the two forms are separated by a relatively sharp geographical discontinuity. On the southern and western sides of the Plateau, intermediate forms are much more frequent. There the geographical changes are more gradual, and broad zones of hybridization are evident. On the western side of the range of *C. berlandieri* subsp. *pinifolius*, numerous plants intermediate in stature and leaf length are found: 25 mi W of Ozona, Crockett Co., Texas, *McVaugh 8209* (LL, TEX). 3 mi S of Camp Barkeley, Taylor Co., Texas, *Tolstead 7096, 41983* (MO, NEB, NY, PO, SMU, UC). 3 mi E of Garden City, Glasscock Co., Texas, *Munz & Gregory 23422* (RSA, UC). Similarly, collections intermediate between *C. berlandieri* subsp. *pinifolius* and the Rio Grande Valley populations of subsp. *berlandieri* are relatively frequent. Several examples are as follows: Ca. 1.9 mi from Del Rio, Val Verde Co., Texas, *Traverse 2162* (SMU, TEX). 9 mi W of Brackettville, Kinney Co., Texas, *McVaugh 7685* (DS, F, SMU, TEX). 6 mi SE of Uvalde, Uvalde Co., Texas, *Munz 13316* (POM).

Over much of its distribution, *C. berlandieri* subsp. *berlandieri* occurs with or near populations of species of sect. *Salpingia*. In most cases of sympatry a few plants of one form are found scattered in or near a colony of the other, and only rarely are both forms common at any locality. The taxa I observed growing together with *C. berlandieri* subsp. *berlandieri* were *C. hartwegii* subsp. *filifolius* in De Baca Co., New Mexico and *C. hartwegii* subsp. *pubescens* in the Texas Panhandle. Also occurring with *C. berlandieri* subsp. *berlandieri* in the Panhandle and in western Oklahoma, but more distinct ecologically, are *C. hartwegii* subsp. *fendleri* and *C. lavandulifolius*. In West Texas there is some likelihood of contact between *C. tubicula* and *C. berlandieri* subsp. *berlandieri*, although their edaphic restrictions seem to reduce this possibility severely. Lastly, local sympatry may also occur with *C. hartwegii* subsp. *maccartii* in the lower Rio Grande Valley, since the edaphic and geographical ranges of the two forms overlap there.

5b. **Calylophus berlandieri** Spach subsp. **pinifolius** (Engelm. ex A. Gray) Towner, comb. nov.—Fig. 5.

Oenothera serrulata Nutt. var. *pinifolia* Engelm. ex A. Gray, Boston J. Nat. Hist. 6: 189. 1850; Munz, Amer. J. Bot. 16: 715. 1929. *Meriolix serrulata* (Nutt.) Raf. (var.) *pinifolia* (Engelm. ex A. Gray) Small, Bull. Torrey Bot. Club 23: 187. 1896. *Oenothera serrulata* subsp. *pinifolia* (Engelm. ex A. Gray) Munz, N. Amer. Fl., ser. 2, 5: 141. 1965.

Oenothera capillifolia Scheele, Linnaea 21: 576. 1848. *Meriolix capillifolia* (Scheele) Small, Fl. S.E. U.S. 846, 1335. 1903. TYPE: United States, Texas, Comal Co., New Braunfels, April (1846?), *Ferdinand Roemer* (not located).

Meriolix hillii Small, Fl. S.E. U.S. 846, 1335. 1903. TYPE: United States, Texas, Edwards Co., Frio Water Hole, 30 June 1895, *R. T. Hill* (NY).

Meriolix melanoglottis Rydb. ex Small, Fl. S.E. U.S. 846, 1335. 1903. *Oenothera serrulata* Nutt. var. *maculata* H. Lév., Monogr. Onoth. 336, 339. 1908 (lectotype: *Heller 1600*, MO). TYPE: United States, Texas, Kerr Co., Kerrville, 19–25 April 1894, *A. A. Heller 1600* (NY, holotype; ARIZ, MO, NEB, NY, PH, POM, RM, SMU, UC, US, isotypes).

Oenothera serrulata Nutt. var. *drummondii* Torr. & A. Gray sensu Munz, Amer. J. Bot. 16: 714. 1929, pro parte. *O. serrulata* subsp. *drummondii* (Torr. & A. Gray) Munz sensu Munz, N. Amer. Fl., ser. 2, 5: 142. 1965, pro parte.

Oenothera serrulata Nutt. var. *drummondii* Torr. & A. Gray f. *flava* Munz sensu Munz, Amer. J. Bot. 16: 714. 1929, for the most part, excluding the type.

Calylophus serrulatus (Nutt.) Raven var. *spinulosus* (Torr. & A. Gray) Shinners sensu Shinners, Sida 1: 339. 1964, pro parte.

Calylophus drummondianus Spach subsp. *drummondianus* sensu Towner in Correll & Johnston, Man. Vasc. Pl. Texas 1123. 1970, all, except for the type.

Annual to short-lived perennial; stems one to several, simple or sparsely branched, suberect to erect, 3–8 dm high. Leaves well spaced, linear to narrowly oblanceolate or narrowly lanceolate, 2.5–9 cm long, 0.2–0.9 cm wide, the margin remotely serrulate to spinuose-serrate; lowest stem leaves narrowly oblanceolate. Sepals with conspicuously keeled midribs, with free tips 0.5–4 mm long. Stigma and inside of floral tube frequently deep blue black in certain populations. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. TEXAS: Comal Co., rocky prairies, New Braunfels, April 1846, *Ferdinand Lindheimer 37 = 394* (GH, holotype; DS, MO, NY, PH, RSA, US, isotypes).

Distribution (Fig. 18): Common on prairies and in open places in oak savanna, on rocky, clay, or sandy soils, often calcareous, from Blaine and Lincoln cos., Oklahoma, south through a narrow portion of north-central Texas to central Texas, where it is widely distributed, especially on the Edwards Plateau; also occurs locally in western and southern Louisiana. Elevational distribution from near sea level (Sulfur, Calcasieu Parish, Louisiana) to ca. 900 m (Sonora, Sutton Co., Texas). Flowers mostly from March to June.

Representative specimens examined:

UNITED STATES. MISSOURI: Jackson Co.: Sheffield (introduced), *Bush 328* (F, GH). OKLAHOMA: Blaine Co.: 3 mi W of Greenfield, *Hopkins & van Valkenburgh 4131* (OKL). Caddo Co.: Rim of Devil's Canyon, *Hopkins et al. 309* (DS, F, MO, OKL, OKLA, RM, SMU, UC, WTU). Canadian Co.: 2 mi W of El Reno, *Munz & Gregory 23505* (RSA, UC, WTU). Cleveland Co.: Norman, *Demaree 12473* (MO, NY, OKL, POM, RM, SMU). Cotton Co.: 6.9 mi E of Walters, *Towner 141* (DS). 9 mi W of Comanche, *Towner 142* (DS). Custer Co.: Ca. 1.5 mi W of Custer, *Towner 154* (DS). Lincoln Co.: 3.2 mi S of Perkins, *Towner 149B* (DS). Logan Co.: 15 mi W of Guthrie, *Raven & Gregory 19462* (DS). 5.4 mi W of Guthrie, *Towner 151* (DS). McClain Co.: Blanchard (Johnson's Pasture), *Demaree 13094* (MO, NY,

OKL, PH, POM, TEX, UC, US). Oklahoma Co.: 6 mi W and 6 N of Oklahoma City, *Waterfall 1423* (OKL, POM). Seminole Co.: SE of Konawa, *Robbins 2458* (OKL, UC). Stephens Co.: S of Comanche, *Waterfall 3679* (NY, OKL). TEXAS: Austin Co.: Bellville, *Fisher 3846* (F). Bastrop Co.: S of Bastrop, *Lundell & Lundell 10355* (ARIZ, LL, POM, US). Bell Co.: 5 mi S of Temple, *Wolff 4037* (F). Bexar Co.: San Antonio, *Clemens & Clemens 686* (NY, PH, POM, RM). Blanco Co.: 2 mi S of Blanco, *Tharp et al. 17T195* (RM, SMU). 5.5 mi N of Johnson City, *Towner 68* (DS). 32.7 mi NW of San Marcos, *Towner 66* (DS). Brown Co.: 8.2 mi S of Brownwood, *Towner 72* (DS). Brownwood, *Ewing 26* (LL, SMU, TEX). Burnet Co.: Burnet, *Fisher 40065* (ARIZ, NEB, TEX). Coke Co.: 2 mi E of Robert Lee, *Shinners 31773* (SMU). Coleman Co.: 14.3 mi N of Coleman, *Towner 74* (DS). Comal Co.: New Braunfels, *Lindheimer 809* (ARIZ, DS, F, GH, MO, NMC, NY, OKL, PH, TEX, UC, US). 20.9 mi NW of San Marcos, *Towner 64* (DS). Comanche Co.: Round Top Mt., *Eggert in 1900* (MO). Coryell Co.: 13 mi E of Gatesville, *Jackson 4* (LL, SMU, TEX). Crockett Co.: 30 mi N of Juno, *Warnock 15289* (LL, TEX). Dallas Co.: White Rock Lake, *Lundell & Lundell 8531* (DS, GH, LL, POM, SMU). Dimmit Co.: Carrizo Springs, *Palmer 33732* (MO). Ellis Co.: 1½ mi N of Midlothian, *Cory 53327* (DS, KANU, RM, SMU, UC). Erath Co.: 3.5 mi W of Stephensville, *Gould 5644* (RSA, SMU, UC). Fayette Co.: La Grange, *Hanisch in 1935* (TEX). Frio Co.: 6 mi NE of Pearsall, *Lundell 13628* (LL, TEX). Gillespie Co.: Bear Mt., *Correll & Correll 12763* (LL, SMU). Hamilton Co.: Hamilton, *Tharp in 1941* (GH). Harris Co.: Houston, *Fisher 3481* (F). Hays Co.: 5 mi W of San Marcos, *Gregory 419* (DS, RSA, US). 5.1 mi NW of San Marcos, *Towner 62* (DS). 7.5 mi NW of San Marcos, *Towner 63* (DS). Hill Co.: 8.5 mi NE of Hillsboro, *Shinners 12494* (SMU). Hood Co.: Grandbury, *"Naples School" 7174* (US). Irion Co.: 30 mi N of Barnhart, *Raven & Gregory 19210* (DS). Karnes Co.: 3 mi SE of Karnes City, *Johnson 857* (RSA, TEX). Kendall Co.: 19 mi S of Fredericksburg, *Munz & Gregory 23438* (RSA, WTU). Kerr Co.: 4 mi SW of Kerrville, *Cory 51763* (DS, SMU). Kimble Co.: No locality, *Tharp 43-738* (TEX, UC). Kinney Co.: Ca. 30 mi SE of Brackettville, *Strother 240* (DS, SMU). Lampasas Co.: 1 mi S of Lampasas, *Whitehouse 15384* (SMU). Llano Co.: No locality, *Lundell & Lundell 9050* (DS, GH, LL, POM, SMU). 1.7 mi N of Llano, *Towner 69* (DS). Medina Co.: Hondo, *Pilsbry in 1903* (PH). Menard Co.: 10.3 mi N of Menard, *Raven & Gregory 19273* (DS). McClennan Co.: Between Waco and McGregor, *York 46074* (TEX, UC). McCulloch Co.: 9 mi SE Brady, *Munz & Gregory 23431* (RSA, UC, WTU). McMullen Co.: No locality, *Schultz 64* (US). Mills Co.: Goldthwaite, *Ferguson 4-21* (MO, PH, TEX, UC). San Saba Co.: 4 mi W of Pontotoc, *Jones 24* (LL, SMU). Sutton Co.: Sonora, *Tharp in 1931* (TEX). Tarrant Co.: Lake Como, *Ruth 30* (F). Travis Co.: 9 mi W of Oak Hill, *Lundell & Lundell 8898* (DS, GH, LL, NY, POM, RM, SMU, UC). Uvalde Co.: 20 mi N of Uvalde, *Graves 9* (RM, RSA). Val Verde Co.: Devil's R. N of Del Rio, *Pilsbry in 1903* (PH). Washington Co.: No locality, *Brackett in 1938* (GH). Williamson Co.: No locality, *York 46193* (TEX). LOUISIANA: Acadia Parish: Prairies near Crowley, *Small & Wherry 11741* (NY). Calcasieu Parish: Sulphur, *Palmer 7719* (MO). St. Mary Parish: Near Berwick, *Small & Wherry in 1925* (NY).

As with *Calylophus berlandieri* subsp. *berlandieri*, subsp. *pinifolius* incorporates portions of several of the taxa recognized by earlier authors. It corresponds rather closely with *Oenothera serrulata* subsp. *drummondii* except for the inclusion of narrow-leaved individuals and exclusion of complex heterozygotes. As mentioned earlier, the types seen of *C. drummondianus* were erroneously assigned to the outcrossing species in a preliminary report (Towner & Raven, 1970). The types actually belong with the complex structural heterozygote *C. serrulatus*, and the name is reduced to synonymy. The collection used as the basis for *Oenothera serrulata* var. *drummondii* f. *flava* was also found to belong with *C. serrulatus*, having the small flowers and half-sterile pollen indicative of complex structural heterozygosity.

Calylophus berlandieri subsp. *pinifolius* is distributed primarily from central Texas to central Oklahoma, inhabiting more mesic areas than does subsp. *berlandieri*. Most typically it is found in calcareous, rocky soil in oak savanna. Colo-

nies occur in open or disturbed areas in that habitat and in prairies. This subspecies is the only member of sect. *Calylophus* occurring on the Edwards Plateau in Texas.

Earlier reference was made to the narrow-leaved variants occurring in the two subspecies of *C. berlandieri*. The presence of these forms in both taxa prevents the use of leaf proportion as a diagnostic or key character. However, *C. berlandieri* subsp. *pinifolius* is distinctly longer leaved than subsp. *berlandieri*, and the use of this character together with differences in stature permits an easy diagnosis of most individuals. Subspecies *pinifolius* generally has a slender taproot and is difficult to maintain for more than a year in the greenhouse, leading to the inference that it is probably a short-lived perennial or annual in the field. This contrasts with subsp. *berlandieri*, which is distinctly perennial over most of its range.

Some representatives of this subspecies possess purplish black stigmas and/or inner surface of the floral tubes. This extremely interesting character is present as a polymorphism in many populations, but is restricted to those in south-central Texas. The dark-pigmented forms are especially frequent in Bexar, Blanco, Comal, Gillespie, Hays, Kendall, Kerr, and Travis cos. Some examples of the variants include the following collections: Type specimen of *Meriolix melanoglottis* Rydb. ex Small. Type specimen of *Meriolix hillii* Small. 19 mi S of Fredericksburg, Kendall Co., Texas, *Munz & Gregory 23438* (RSA, WTU). 7.5 mi NW of San Marcos, Hays Co., Texas, *Towner 63* (DS; most plants with black stigma, some with black hypanthium). 5.5 mi N of Johnson City, Blanco Co., Texas, *Towner 68* (DS; plants with black stigma only). U.S. 87 near NW city limits of San Antonio, Bexar Co., Texas, *Klein 1671–1674* (DS). New Braunfels, Comal Co., Texas, *Lindheimer 809* (ARIZ, DS, F, GH, MO, NMC, NY, OKL, PH, TEX, UC, US). 4 mi SW of Kerrville, Kerr Co., Texas, *Cory 51763* (DS, SMU).

Plants from populations of *C. berlandieri* subsp. *pinifolius* from Oklahoma differ modally from those in Texas in having shallower leaf serrations and more strigose pubescence on the upper stems. This is especially apparent in the northernmost populations, e.g., those in Logan, Oklahoma, McClain, and Cleveland cos. In regard to stature, leaf dimensions, and most other characters, these plants are identical to individuals from Texas populations of subsp. *pinifolius*. Some of the largest-flowered members of the species occur in these Oklahoma populations. Examples of plants from this area are as follows: 5.4 mi W of Guthrie, Logan Co., Oklahoma, *Towner 151* (DS). Norman, Cleveland Co., Oklahoma, *Demaree 12767* (OKL, POM, SMU). Blanchard, McClain Co., Oklahoma, *Demaree 13094* (MO, NY, OKL, PH, POM, TEX, UC, US).

As in *C. berlandieri* subsp. *berlandieri*, this subspecies has a great deal of translocation heterozygosity. Of the 30 plants which have been examined, 24 or 80% had ring or chain multivalents at meiotic metaphase I. Of these plants, those having 1 or 2 heterozygosities were the most frequent types. The average number per plant was 1.6.

Floral behavior has been observed in Brown Co., Texas (*Towner 72*) and in the greenhouse at Stanford, California. Anthesis took place shortly after sun-

rise. Insect visitors to flowers observed by me, and by P. H. Raven and D. P. Gregory in Hays and Kyle cos., Texas (personal communication), included small butterflies, flies, skippers [*Atalopedes campestris* (Boisduval)], a variety of beetles, especially cantharids and *Acmaeodera* (Buprestidae), numerous small bees (*Agapostemon, Augochlorella, Dialictus, Evylaeus,* and *Halictus*), and a few large and medium-sized bees (*Apis, Bombus, Megachile, Xylocopa,* anthophorids). It seems likely that a broad spectrum of insects serves as pollen vectors. Skippers, medium-sized bees, and beetles, judged by their abundance, size, and contact with the anthers and stigma, may be the primary pollinating agents for most populations. The black floral tubes and stigmas, which occur together with large ultraviolet patterns, may complement those patterns in facilitating the orientation of visiting insects. This would be especially important for any species of insect which lacked the tricolor vision of bees and could not discriminate in the ultraviolet region of the spectrum.

With no evidence of hybridization, *C. berlandieri* subsp. *pinifolius* occurs together with *C. hartwegii* subsp. *pubescens* in much of its range in central and west-central Texas. No other member of sect. *Salpingia* overlaps significantly in distribution with subsp. *pinifolius*. Minor geographic sympatry exists in southern Texas with *C. hartwegii* subsp. *maccartii* and in western Texas with *C. tubicula* subsp. *tubicula* and *C. hartwegii* subsp. *filifolius*. In these cases, local sympatry is quite infrequent or absent, probably as a result of habitat segregation.

6. **Calylophus serrulatus** (Nutt.) Raven, Brittonia 16: 286. 1964.—Fig. 6.

Oenothera serrulata Nutt., Gen. N. Amer. Pl. 1: 246. 1818. *Meriolix serrulata* (Nutt.) Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. 1819. *Calylophus nuttallii* Spach, Hist. Nat. Vég. Phan. 4: 350. 1835. *Oenothera serrulata* var. *nuttallii* (Spach) Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. *Meriolix serrulata* var. *nuttallii* (Spach) Walp., Repert. Bot. Syst. 2: 79. 1843. *Oenothera serrulata* var. *typica* Munz, Amer. J. Bot. 16: 712. 1929. *Calylophus serrulatus* (Nutt.) Raven var. *serrulatus*; Shinners, Sida 1: 338. 1964. *Oenothera serrulata* subsp. *serrulata*; Munz, N. Amer. Fl., ser. 2, 5: 141. 1965.

Oenothera leucocarpa Comien ex Lehm. in Hooker, Fl. Bor. Amer. 1: 210. 1833. *O. serrulata* Nutt. var. *douglasii* Torr. & A. Gray, Fl. N. Amer. 1: 502. 1840. *Meriolix serrulata* (Nutt.) Raf. var. *douglassii* (Torr. & A. Gray) Walp., Repert. Bot. Syst. 2: 79. 1843. TYPE: Canada, Saskatchewan, common on limestone rocks on Red and Assiniboine rivers, August 1827, *David Douglas* (K, lectotype).

Calylophus drummondiana Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 272. 1835. *Oenothera serrulata* Nutt. var. *drummondii* Torr. & A. Gray, Fl. N. Amer. 1: 502. 1840. *O. spachiana* Steud., Nom. Bot., ed. 2. 2: 207. 1841. *Meriolix serrulata* (Nutt.) Raf. var. *drummondii* (Torr. & A. Gray) Walp., Repert. Bot. Syst. 2: 79. 1843. *M. drummondiana* (Spach) Small, Fl. S.E. U.S. 846, 1335. 1903. *Oenothera serrulata* subsp. *drummondii* (Torr. & A. Gray) Munz, N. Amer. Fl., ser. 2, 5: 142. 1965, pro parte. *Calylophus drummondianus* subsp. *drummondianus*; Towner in Correll & Johnston, Man. Vasc. Pl. Texas 1123. 1970. TYPE: United States, Texas, along the Rio Brazos on the Texas coastal plain, probably between Brazos Co. and the coast, 1833, *Thomas Drummond* (P, holotype; GH, NY, isotypes, but not *Drummond III. 79* at PH).

Oenothera serrulata Nutt. var. *spinulosa* Torr. & A. Gray, Fl. N. Amer. 1: 502. 1840. *Meriolix serrulata* (Nutt.) Raf. var. *spinulosa* (Torr. & A. Gray) Walp., Repert. Bot. Syst. 2: 79. 1843. *M. spinulosa* (Torr. & A. Gray) Heller, Contr. Herb. Frankl. & Marsh. 1: 70. 1895. *Calylophus serrulatus* (Nutt.) Raven var. *spinulosus* (Torr. & A. Gray) Shinners, Sida 1: 339. 1964. TYPE: United States, Oklahoma, vicinity of the Red R., probably near present-day Choctaw Co., May–June 1819, *Thomas Nuttall*, Torrey Herb. [NY, lectotype; PH, NY, isolectotypes, but not "Red River, Nuttall," (GH), or "Arkansas," (PH)]. Some of Nuttall's Red River and Arkansas collections, such as the GH specimen cited, are actually

Calylophus berlandieri. The type sheet has the Leavenworth specimen cited by Torrey and Gray mounted next to the Red River type of Nuttall.

Meriolix intermedia Rydb. ex Small, Fl. S.E. U.S. 846, 1335. 1903. TYPE: United States, Missouri, Atchison Co., Watson, 7 June 1894, *B. F. Bush 321* (NY, holotype; MO, OKL, isotypes).

Oenothera serrulata Nutt. var. *integrifolia* H. Lév., Monogr. Onoth. 337, 339. 1908. TYPE: United States, probably from southeastern Colorado, 1945, third expedition of John C. Fremont, *no. 47* (MO); Munz, Amer. J. Bot. 16: 713. 1929.

Oenothera serrulata Nutt. var. *drummondii* Torr. & A. Gray f. *flava* Munz, Amer. J. Bot. 16: 714. 1929. TYPE: United States, Texas, Walker Co., Huntsville, *B. C. Tharp 866* (POM-32801; other collections cited in the protologue are *C. berlandieri* subsp. *pinifolius*).

Meriolix oblanceolata Rydb., Brittonia 1: 93. 1931. TYPE: United States, Kansas, Comanche Co., along road 2 mi W of Coldwater, 8 July 1929, *P. A. Rydberg & R. Imler 737* (NY, holotype; KANU, NEB, NY, isotypes).

Calylophus serrulatus (Nutt.) Raven var. *arizonicus* Shinners, Sida 1: 338. 1964. TYPE: United States, Arizona, Navajo Co., dry sandy riverbank 4 mi upstream from White River, 25 June 1951, *S. J. Preece, Jr. & B. L. Turner 2692* (SMU).

Calylophus australis Towner & Raven, Madroño 20: 243. 1970. TYPE: United States, Texas, Cameron Co., Texas route 4, 2.8 mi W of end of road at Boca Chica, 29 May 1969, *Towner 187* (DS-612434, holotype; RSA, TEX, US, isotypes).

Similar to *Calylophus berlandieri.* Herbaceous to suffrutescent perennial from a woody caudex; stems few to many, 1–6 dm high. Floral tube 2–12(–16) mm long, 3–12 mm wide, never blue black within. Sepals 1.5–9 mm long, 2–6 mm wide. Petals 5–12(–20) mm long, 5–15(–20) mm wide. Episepalous filaments 1–5(–7) mm long, the epipetalous filaments 0.5–3 mm long; anthers 1.5–4 (–7) mm long; pollen grains 30–80% aborted. Style 2–15(–20) mm long; stigma 1–2 mm broad, not exserted beyond the anthers, and often in contact with the anthers at the apex of the floral tube, never blue black; ovary 4–13 mm long. Self-compatible and highly autogamous. Gametic chromosome number, $n = 7$, with a ring of 14 chromosomes or a ring of 12 plus a bivalent at meiotic metaphase I.

TYPE: UNITED STATES. Plains along the Missouri River, probably just north of the Platte River in eastern Nebraska, April or May 1811, *Thomas Nuttall* (PH). From Bradbury's account of the expedition (McKelvey, 1955: 115–118) and because of the immature appearance of the type, these dates seem more likely than June, the date of flowering given in the original description.

Distribution (Fig. 19): Common on plains, in grassy open areas in woods, or, rarely, in mountains, usually on sandy or rocky soils, from southern Alberta, southern Saskatchewan, and southern Manitoba to eastern New Mexico, the Texas Panhandle, and the Gulf Coast of Texas, including eastern Montana, eastern Wyoming, eastern Colorado, North Dakota, South Dakota, Nebraska, Kansas, western and central Oklahoma, western and southern Minnesota, Iowa, northwestern Missouri, and with outlying populations in southeastern Wisconsin, northwestern peninsular Michigan, east-central Arizona, and west-central Chihuahua, Mexico. Elevational distribution from sea level along the Texas coast to 2,100 m (18 mi N of Rubio, Chihuahua). Flowers March to August.

Representative specimens examined:

CANADA. ALBERTA: Near Peigan, *Moss 871* (DAO, NY). SASKATCHEWAN: Katepwa, *Russell 54519* (DAO). Pilot Butte, *Hart in 1939* (DAO, UC). 13 mi W of Saskatoon, *Shumovich 38* (CAN, DAO, RM). Moose Jaw, *Turner 48* (GH, NY, POM, RSA). MANITOBA:

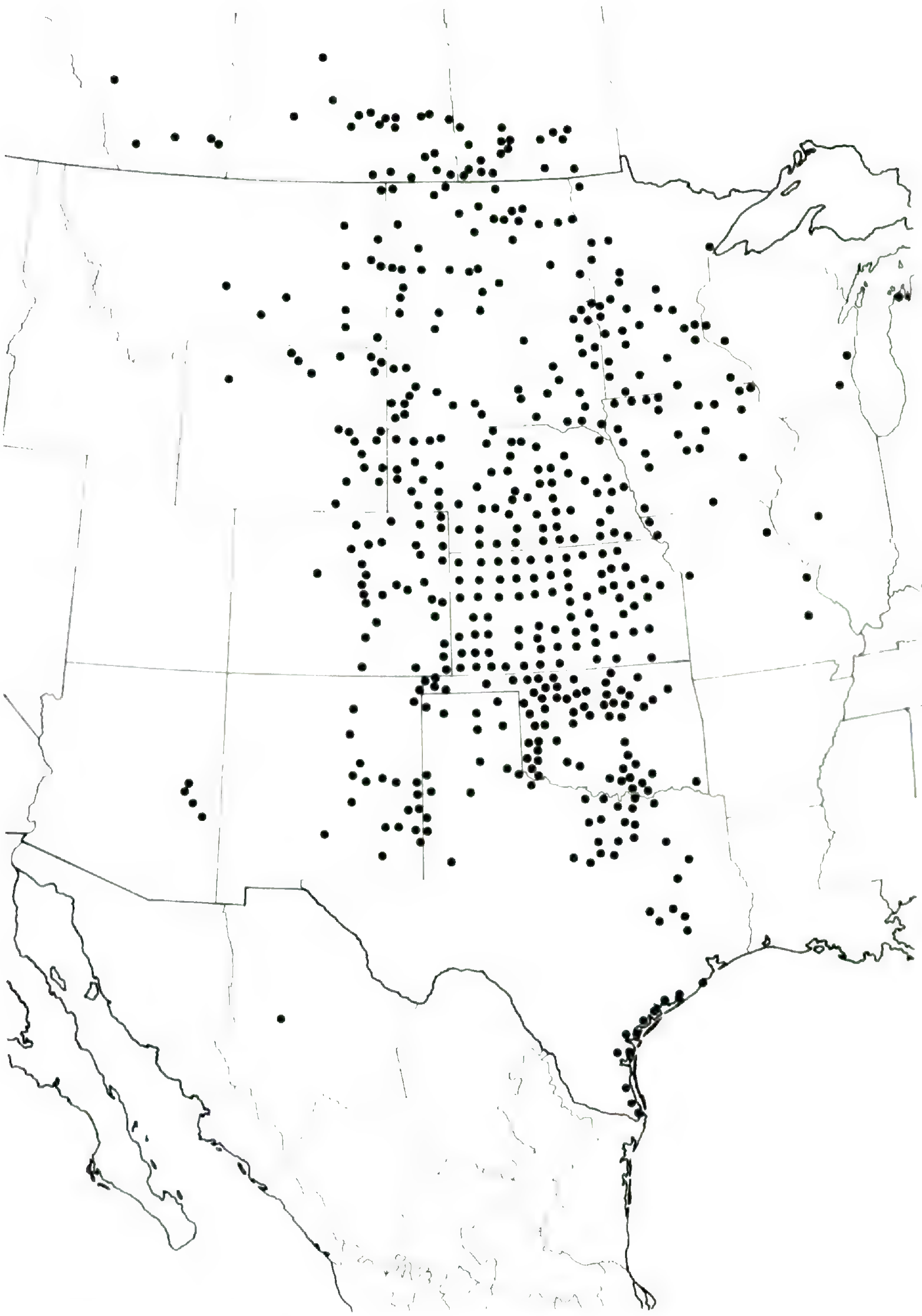


FIGURE 19. Distribution of *Calylophus serrulatus*.

Brandon, *Fowler in 1887* (DAO, MO, NY, US). Horton, *Love & Love 6081* (DAO, GH). Melita, *Scoggan 9794* (CAN, GH). Mouth of the Qu'Appelle R., *Macoun & Herriot 72,377* (F, GH, NY).

UNITED STATES. MONTANA: Billings Co.: 1.5 mi S of Medora, *Stephens & Brooks 13486*

(KANU). Powder River Co.: 15 mi NW of Boradus, *Booth 2517* (KANU, WTU). Prairie Co.: 32 mi NW of Terry, *Stephens & Brooks 23691* (DS). Sheridan Co.: Westby, *Larsen 213* (GH, NY). Wheatland Co.: 12 mi S of Harlowton, *Hitchcock 2429* (MO, POM, RSA). NORTH DAKOTA: Barnes Co.: Valley City, *Stevens in 1934* (F, RM, UC). Divide Co.: Alkabo, *Larsen 88* (GH, MO, PH). Dunn Co.: 10 mi NW of Killdeer, *Stephens & Brooks 12734* (DS, KANU). Golden Valley Co.: 1 mi E and 1 S of Sentinel Butte, *Stephens & Brooks 23428* (DS). Slope Co.: 7 mi S of Amidon, *Cutler 2615* (DS, MO, NY). Ward Co.: 9 mi NW of Minot, *Stephens & Brooks 12897* (DS, KANU). SOUTH DAKOTA: Custer Co.: 14 mi S of Pringle, *Stephens & Brooks 13798* (DS, KANU). Harding Co.: 6 mi N, 11 W, and 2 N of Ludlow, *Stephens & Brooks 13657* (DS, KANU). Lawrence Co.: 0.8 mi N of Spearfish, *Mosquin & Mulligan 5160* (DS). Meade Co.: Near Fort Meade, *Forwood 130* (CAN, US). Pennington Co.: Rapid City, *Rydberg 708* (F, GH, NEB, NY, US). Perkins Co.: 10 mi E and 1 S of Bison, *Stephens 7999* (KANU, SMU). MINNESOTA: Chippewa Co.: Montevideo, *Moyer in 1908* (NY, UC). Dakota Co.: 5.5 mi W of Hastings, *Moore 15797* (DAO, GH). Faribault Co.: Elmore, *Pammel 596* (GH, MO, RM, US). Nicollet Co.: No locality, *Aiton in 1891* (F, NY, POM, US). Ottertail Co.: Perham, *Chandonnet in 1910, 1911* (GH, RM). Yellow Medicine Co.: S side of Granite Falls, *Moore 13071* (SMU, UC). WISCONSIN: Pepin Co. (?): Lake Pepin, *Hale 1861* (F, MO). WYOMING: Converse Co.: 15 mi N of Douglas, *Stephens & Brooks 23965* (DS). Crook Co.: 5 mi NE of Hulett, *Porter & Porter 9564* (CAN, DS, RM, RSA, UC, WTU). Goshen Co.: 12 mi W of Lagrange, *Stephens & Brooks 22947* (DS). Niobrara Co.: 10 mi N of Lusk, *Mosquin & Mulligan 5142* (DS). Platte Co.: Guernsey, *Nelson 8268* (DS, F, GH, MO, NEB, NY, POM, RM, RSA, UC, US). 3 mi W of Guernsey, *Porter 4903* (COLO, DS, GH, MO, PH, RM, RSA, SMU, TEX, WTU). NEBRASKA: Adams Co.: 20 mi W of Hastings, *Mathias 308* (MO, POM). Chase Co.: 6 mi N of Imperial, *Stephens & Brooks 11490* (KANU). Cherry Co.: Vicinity of Hackberry Lake, *Dworak in 1912* (NEB). Dawes Co.: Chadron State Park, *Porter & Porter 8807* (DS, RM, WTU). Garden Co.: 2 mi S of Lewellen, *Stephens & Brooks 11557* (KANU). Greeley Co.: 9 mi N of Greeley, *McGregor 19344* (KANU). Hayes Co.: 14 mi W of Hayes Center, *Stephens & Brooks 13958* (DS, KANU). Holt Co.: 12.5 mi S of Atkinson, *Stephens 15579* (KANU). Kearney Co.: Minden, *Hapeman in 1930* (OKLA, TEX). Lincoln Co.: North Platte, *Jones in 1925* (DS, POM). Morrill Co.: 27 mi N of Broadwater, *Stephens & Brooks 13888* (DS, KANU). Saunders Co.: 4 mi S of Valparaiso, *Croat 2126, 2127* (KANU, MO). Sheridan Co.: 13.5 mi S of Hay Springs, *Stephens & Brooks 13839* (DS, KANU). Webster Co.: S of Blue Hill, *Tolstead 411245* (NEB, UC). IOWA: Emmet Co.: No locality, *Cratty, s.n.* (DS, F, NY, PO, UC). Fremont Co.: Hamburg, *Bush 10313* (GH, MO, PH, POM). Lyon Co.: Gitchie Manitou State Park, *Thorne 14234* (SMU, UC). Palo Alto Co.: Highland Township, *Hayden 10081* (PH, UC, US). Wayne Co.: Corydon City Reservoir, *van Bruggen 2716* (UC). COLORADO: Baca Co.: 23 mi S of Walsh, *Stephens & Brooks 21788* (DS). Cheyenne Co.: 17 mi N of Kit Carson, *Stephens & Brooks 22662* (DS). Douglas Co.: Wolhurst, *Clokey 3827* (CAN, DS, F, GH, MO, NY, PH, POM, RM, SMU, UC, US, WTU). Elbert Co.: 4 mi SW of Limon, *Ownbey 1301* (COLO, GH, MO, NY, RM, UC). Kiowa Co.: 1 mi E of Eads, *Stephens & Brooks 22703* (DS). Kit Carson Co.: 5 mi E of Flagler, *Stephens & Brooks 22641* (DS). Logan Co.: E of Sterling, *Mathias 333* (MO, POM). Phillips Co.: 5 mi S of Holyoke, *Stephens & Brooks 24072* (DS). Prowers Co.: 20 mi S and 7 W of Holly, *Stephens & Brooks 21931* (DS). Sedgwick Co.: 1 mi S of Julesburg, *Stephens & Brooks 24059* (DS). Yuma Co.: Wray, *Eggleston in 1919* (F, MO, POM). KANSAS: Barber Co.: 3 mi W and 5 mi N of Medicine Lodge, *McGregor 14430* (KANU, SMU, US). Clark Co.: 8 mi S of Sitka, *Rydberg & Imler 766* (KANU, MO, NY). Ellis Co.: 2 mi W of Hays, *Bondy 97* (ARIZ, CAN, F, GH, OKL, OKLA, PH, RM, SMU). Ellsworth Co.: 1 mi N and 1 W of Kanapolis, *Fearing & Latham in 1950* (GH, KANU, TEX, US). Ford Co.: Ca. 5 mi WNW of Dodge City, *Towner 159* (DS). Grant Co.: High upland prairies, *Thompson 1* (CAN, F, NY, UC, US). Harvey Co.: 8.5 mi E of Newton, *Harms 1633* (SMU, UC). Kearney Co.: 5 mi E of Kendall, *Rydberg & Imler 1059* (KANU, NY). Kingman Co.: 3 mi E of Kingman, *Stephens 11127* (OKLA). Meade Co.: 11 mi E of Meade, *Hubert 3593* (KANU, OKLA). Montgomery Co.: 2 mi S of Sycamore, *McGregor 12839* (KANU, NY). Pottawatomie Co.: State Park No. 2, *Marsh 1725* (KANU, SMU, US). Riley Co.: Stony hills, *Norton 168* (GH, MO, NMC, NY, RM, US). 12 mi N of Manhattan, *Raven & Gregory 19483* (DS). Scott Co.: 10.6 mi N of Scott City, *Towner 160* (DS). Smith Co.: 2 mi W of Cedar, *Horr E131* (COLO, F, GH, KANU, LL, OKL, OKLA, RM, SMU, UC, US). Wilson Co.: 3 mi NW of Neodesha, *McGregor 4306* (GH, KANU, US). MISSOURI: Atchison Co.: No locality, *Bush 10321* (GH, PH, POM). Iron Co.: Deo Arc, *Smith 460* (F). OKLAHOMA: Alfalfa Co.: 3 mi N and 7.8 E of Cherokee,

Stratton 6371 (OKL, OKLA). Atoka Co.: No locality, *Hopkins et al. 1132* (OKL, RM, WTU). Blaine Co.: Roman Nose State Park, *Goodman & Waterfall 4189* (OKL, OKLA). 21.5 mi W of Kingfisher, *Towner 153* (DS). Carter Co.: 4 mi N of Springer, *Waterfall 705* (OKL, OKLA, POM). 11.5 mi S of Davis, *Towner 144* (DS). Ca. 7 mi E of Fox, *Towner 143* (DS). Cimarron Co.: 4 mi N of Kenton, *Rogers 5697* (OKL, TEX, US). Comanche Co.: Boggy Hollow Creek, *Eskew 1743* (OKL, OKLA). Dewey Co.: W of Vici, *Goodman 2573* (GH, MO, NY, OKL, POM, RM, WTU). Ellis Co.: Near Shattuck, *Clifton 3155* (GH, NY, OKLA). Greer Co.: 2 mi S of Mangum, *Robbins 3035* (OKL, SMU, UC). 6 mi S of Mangum, *Towner 80* (DS). 2.7 mi S of Mangum, *Towner 83* (DS). Harmon Co.: 13.5 mi W of Mangum, *Waterfall 7766* (OKL, OKLA, TEX). Harper Co.: Near Buffalo, *Stevens 536* (DS, GH, NY, OKL, OKLA, SMU). Kingfisher Co.: 8 mi E of Okeene, *Kelting 250* (KANU, OKL, UC). Lincoln Co.: 6.5 mi S of Perkins, *Towner 148* (DS). 3.2 mi S of Perkins, *Towner 149a* (DS). Logan Co.: 18.8 mi N of Guthrie, *Towner 150* (DS). Major Co.: Togo, *Demaree 12370* (MO, POM). 1.7 mi NE of Orienta, *Raven & Gregory 19471* (DS). Murray Co.: Davis, *Demaree 12508* (GH, MO, NY, OKL, PH). Turner Falls, *Cory 59044* (OKLA, SMU). 6.2 mi E and 2.3 N of Sulfur, *Towner 146* (DS). 8.1 mi S of Davis, *Towner 145* (DS). Oklahoma Co.: 2 mi W of Wood, *Waterfall 2772* (GH, OKL, OKLA). Pontotoc Co.: 1.5 mi NE of Lawrence, *Robbins 2995* (OKL, SMU, UC, WTU). Roger Mills Co.: Ca. 8 mi E of Strong City, *Towner 155* (DS). Tulsa Co.: W of Tulsa, *McKelvey 2508* (GH, POM). Woods Co.: Between Cimarron and Waynoka, *Goodman & Waterfall 4229* (COLO, KANU, OKL, OKLA). TEXAS: Anderson Co.: Palestine, *Palmer 13426* (MO). Andrews Co.: 21–23 mi NE of Andrews, *Correll 32786* (LL). Aransas Co.: 4.6 mi NE of Rockport, *McCart 5566* (TEX). Copano Bay, sandy beach, *Bogusch S-75* (US). 1.3 mi W of Copano Village, near shore of Copano Bay, *Towner 182* (DS). Armstrong Co.: Ca. 10 mi NE of Wayside, *Rowell 5402a* (OKLA). Austin Co.: Colbert's Station, Industry, *Sheldon 3575* (F). Bailey Co.: 5 mi NW of Muleshoe, *Correll 13105, 13106* (LL, SMU). Brazoria Co.: 11.6 mi S of San Luis Pass Bridge on road to Surfside, *Towner 173* (DS). Brazos Co.: College Station, *Parks in 1946, 1947* (RSA, TEX). NW of Bryan, in prairie, *Lundell & Lundell 11304* (POM, SMU). 3.5 mi S of College Station, *McVaugh 6997* (F, LL, SMU). Calhoun Co.: Magnolia Beach, *Tharp in 1930* (TEX). 0.1 mi from shore at Magnolia Beach, *Towner 178* (DS). Cameron Co.: Stover Point, Laguna Atascosa National Wildlife Refuge, *Traverse 1125* (SMU, TEX). Boca Chica, *Lundell & Lundell 8617* (DS, GH, LL, NY, POM, SMU). Brownsville, *Fisher 41188* (ARIZ, NEB). 0.8 mi N of bridge from mainland on Padre I., *Towner 189* (DS). Childress Co.: 10 mi N of Childress, *Correll & Johnston 16876* (LL). Cochran Co.: 14 mi N of Bronco, *Towner 137* (DS). 10.3 mi N of Bronco, *Towner 136* (DS). Collin Co.: Near Plano, *Lundell & Lundell 9313* (DS, GH, LL, POM, SMU). Cooke Co.: 5 mi N of Gainesville, *Gould 6867* (MO, SMU, TEX, UC). Dallam Co.: 1 mi SE of Texline, *York & Rodgers 192* (SMU, TEX, UC). Dallas Co.: Dallas, *Reverchon 3563* (NY). Denton Co.: 5 mi N of Denton, *Cory 57359* (SMU). Eastland Co.: Ranger, *Robinson in 1931* (POM). Erath Co.: Stephensville State Park, *Hoisington in 1946* (TEX). Fannin Co.: Bonham, *Milligan s.n.* (NMC). Galveston Co. (?): Galveston I., *Bechdolt in 1870* (PH). Gray Co.: McLean, *Craig in 1934* (POM). Grayson Co.: Near Gunter, *van Meter 18* (SMU). Hale Co.: 7 mi S of Plainview, *Gould 7156* (SMU). Hall Co.: Memphis, *Thames 7192* (TEX, US). Hardeman Co.: Acme, *Russel 88* (TEX). Hartley Co.: 3 mi SE of Dalhart, *Cory 32667* (POM). Hood Co.: Near Center Mills, *Blackwell 26* (NY, SMU). Hutchinson Co.: Borger, *Hope 4* (LL). Jack Co.: 2.5 mi NE of Jacksboro, *Hennen 421* (SMU). Jackson Co.: 11.2 mi W of Palacios, *Towner 175* (DS). Johnson Co.: S of Rio Vista, *Lewis 4* (SMU). Kleberg Co.: Beach along Laguna Madre, Laureles Division of King Ranch, *Johnston 53224.13* (TEX). Padre I., *Cory 49120* (GH, LL, SMU). Madison Co.: 3 mi N of North Zulch, *Morgan 39* (TEX). Matagorda Co.: 6.5 mi S of Matagorda, *Towner 174* (DS). Montague Co.: 4 mi N of Nocona, *Whitehouse 10070* (SMU). Montgomery Co.: Willis, *Warner s.n.* (MO). Nueces Co.: Corpus Christi, *Drushel 8932* (MO, NY, US). Corpus Christi, *Heller 1517* (PH, US). Parker Co.: Weatherford, *Tracy 7820* (F, GH, MO, NEB, NY, TEX, US). Parmer Co.: 7.8 mi NW of Farwell, *Rowell 10023* (DS, RSA). Refugio Co.: 4.1 mi SE of Austwell, *Towner 181* (DS). Robertson Co.: 3–4 mi S of Hearne, *Reeves 930* (POM). San Patricio Co.: 2 mi S of Ingleside, *Cutler 920* (OKL, WTU). 3.5 mi S of Ingleside, ca. 0.5 mi from Corpus Christi Bay, *Towner 184* (DS). Smith Co.: Troupe, *Reverchon 2744* (MO, US). Tarrant Co.: Sandy soils, *Reverchon 913* (F, GH, KANU, NEB, NY, PH, UC). Van Zandt Co.: 3 mi E of Wills Point, *Shinners 12381* (COLO, SMU). Walker Co.: Vicinity of Huntsville, *Dixon 569* (F, POM, RM, US). Wise Co.: Near Park Springs, *McCart 1633* (SMU, TEX). NEW MEXICO: Chaves Co.: 8.3 mi W of Caprock, *Towner 134* (DS). De Baca Co.: 11 mi S of Ft. Sumner, *Towner 131* (DS). Eddy

Co.: Lakewood, *Wooton in 1909* (NMC, US). Guadalupe Co.: Halfway between Anton Chico and Santa Rosa, *Arsène & Benedict 16681* (POM, US). Lea Co.: Knowles, *Wooton in 1909* (NMC, US). Roosevelt Co.: 5 mi NE of Portales, *Goodman & Hitchcock 1119* (DS, F, GH, MO, NY, PH, POM, RM, UC). 14.0 mi SW of Elida, *Towner 133* (DS). 8.0 mi E of Taiban, *Towner 132* (DS). San Miguel Co.: Between Las Vegas and Romeroville, *Arsène & Benedict 15458* (POM, US). Union Co.: Perico, *Bartlett 227* (NMC). ARIZONA: Graham Co.: Willow Spring, *Palmer 481* (GH, US). Navajo Co.: 4 mi N of Carrizo, *Pulta & Phillips 1008* (ARIZ, UC). 4 mi SW of Show Low, *Lehto 1072* (ARIZ). Forestdale, 66 mi S of Holbrook, *Slough 83* (US).

MEXICO. CHIHUAHUA: 18 mi N of Rubio, District of Cusihuiriachic, *Shreve 7960* (POM, US). TAMAULIPAS: Coastal dunes near Río Grande, *Le Sueur 328* (probably of this species, ARIZ, F, TEX).

This species, the earliest described, cultivated, and illustrated (Hooker, 1825) taxon of *Calylophus*, occurs widely over the North American Plains, and is the most familiar member of the genus, although its breeding system has only recently been described (Towner, 1970b). Permanent translocation heterozygosity, half-sterility of pollen and ovules, self-compatibility, and small flowers enhancing self-fertilization are present in *C. serrulatus* as part of the genetic system of complex structural heterozygosity. This type of breeding system is frequent in the Onagraceae, but in *Calylophus* is restricted to this species. Characters associated with this breeding pattern are used as the primary basis for distinguishing *C. serrulatus* from *C. berlandieri*.

Whether factor complexes exist and are maintained in *C. serrulatus* by gametic lethals was not determined. The presence of gametophytic half-sterility makes the involvement of gametic lethals appear likely, but does not exclude mechanisms utilizing megaspore competition and/or zygotic lethals. Although unlikely, the observed levels of pollen and ovule sterility may stem from random chromosome disjunction and the resulting genetic deficiencies and duplications in the gametes. There were no consistent reciprocal differences in pollen fertility, morphology, or chromosomal configurations in hybrids between *C. serrulatus* and *C. berlandieri*, results which would be expected if gametic lethals regulated the transmission of factor complexes. A system utilizing self-sterility alleles combined with egg lethals (see Steiner, 1956, 1957) does not seem to be operating in *C. serrulatus*. All reciprocal crosses between *C. serrulatus* and the self-incompatible species *C. berlandieri* produced only self-compatible hybrids, whereas some self-sterile progeny would be predicted if *C. serrulatus* had retained a functional self-sterility allele.

The flowers of *C. serrulatus* are generally identical to those of *C. berlandieri* except for their smaller size, relatively shorter filaments and style, and the position of the stigma. The placement of the stigma among or near the anthers and early dehiscence of the anthers frequently causes flowers to self-pollinate before anthesis. Undisturbed flowers in the greenhouse showed a high level of autogamous seed set. The similarity of the flowers of the two species extends to morning anthesis times and the ultraviolet-absorbing areas on the petals, stigma, and stamens. Morning anthesis had been known from the first observation of the species by Nuttall (in Hooker, 1825), and was seen and reported again by Stevens (1920), but this was apparently not known to Munz (1965) or Raven (1964). Both mentioned only vespertine anthesis for *Calylophus*. Insects do not

seem to visit *C. serrulatus* frequently. Stevens (1920) observed that bees ignored *C. serrulatus*, although they were active on nearby plants of *Gaura* and *Oenothera*. In my own collecting at 31 colonies of *C. serrulatus*, done at all times of day, no insects were observed visiting flowers. Halictid bees (*Agapostemon*, *Evylaeus*, *Dialictus*) were observed during the morning at one population in Major Co., Oklahoma (P. Raven, personal communication), however.

Meiotic configurations of 34 individuals from 28 populations consisted of a definite or probable ring or chain of 14 chromosomes. Five plants had a ring or chain of 12 chromosomes plus 1 bivalent. Seventeen plants from 5 populations were examined and found to be self-compatible. In *Calylophus* the correlation of self-compatibility and complex structural heterozygosity was found to be nearly perfect. Two exceptions were individuals of *C. berlandieri* having a ring of 12 plus a bivalent at meiotic metaphase I.

With a broad range of phenetic variation which largely overlaps that of *C. berlandieri*, *C. serrulatus* cannot be reliably diagnosed without the use of floral characters or pollen fertility. Parallel geographical variation in vegetative parts is such that near most areas of contact, the two species are quite similar. This implies that *C. serrulatus*, almost certainly a derivative of *C. berlandieri*, is of multiple origins, has experienced secondary local introgression from the parental species or has responded in a similar fashion to natural selection. Much of this vegetative variation in *C. serrulatus* follows a smooth east–west cline, whereas the variation is more discontinuous in *C. berlandieri*. Thus the discontinuities in the parent species are not reflected in the derivative.

Populations formerly assigned to *C. australis*, because they closely resemble adjacent populations of *C. berlandieri*, and by their relative geographical separation from the bulk of *C. serrulatus*, may be an exception to the introgression hypothesis. They could well have been independently derived from *C. berlandieri*. In this paper they are synonymized because no firm knowledge is available on the phylogeny of other populations of *C. serrulatus*. Thus, to preferentially recognize *C. australis*, with scant genetic or morphological support, is to ignore possible polyphyly in the rest of *C. serrulatus*. Instead, *C. serrulatus* is best recognized as a complex assemblage of populations having a common breeding system. These populations encompass a broad morphological diversity, and some of them may have been evolved separately from the bulk of the species.

Variation in *C. serrulatus* involves leaf size and shape, stature, pubescence, and flower size. Flower size is variable throughout the geographical range. Some of the largest-flowered forms occur near large-flowered populations of *C. berlandieri* subsp. *pinifolius* in central Oklahoma. Although the vegetative characters are clinally distributed, most populations occurring west of approximately 98°W longitude are comprised of well-branched, short-leaved, and relatively low-statured plants. East of that line plants are generally less branched, taller and more erect, long leaved, and more densely strigose-canescent.

A few representatives of the eastern form are the following: Davis, Murray Co., Oklahoma, *Demaree 12508* (GH, MO, NY, OKL, PH). Elmore, Farribault Co., Minnesota, *Pammel 596* (GH, MO, RM, US). Near Plano, Collin Co., Texas, *Lundell & Lundell 9313* (DS, GH, LL, POM, SMU). Examples of the western

phenotypes are: 1 mi S of Texline, Dallam Co., Texas, *York & Rogers 192* (SMU, TEX, UC). Wolhurst, Douglas Co., Colorado, *Clokey 3827* (CAN, DS, F, GH, MO, NY, PH, POM, RM, SMU, UC, US, WTU). Moose Jaw, Saskatchewan, *Turner 48* (GH, NY, POM, RSA). Representatives of the coastal Texas populations formerly assigned to *C. australis* include all specimens cited above from Brazos, Austin, Galveston, Brazoria, Matagorda, Jackson, Calhoun, Refugio, Aransas, San Patricio, Nueces, Kleberg and Cameron cos.

Observed instances of direct contact between *C. serrulatus* and *C. berlandieri* were rare. No hybrid zones or populations were identified unequivocally, and the two species were locally allopatric. The only evidence obtained concerning possible mixed populations or direct contact came from the following collections: 3.2 mi S of Perkins, Lincoln Co., Oklahoma, *Towner 149* (DS), one short-styled plant seen in a population of long-styled *C. berlandieri* subsp. *pinifolius*, one of which had a ring of 12 chromosomes and one pair at meiosis. 11.1 mi S of Perryton, Ochiltree Co., Texas, *Towner 158* (DS), chromosome counts of 3 pairs + ring of 4, and possible ring of 12 + 1 pair from the same population, thus perhaps some individuals of *C. serrulatus* in a population of *C. berlandieri* subsp. *berlandieri*. 11.2 mi W of Palacios, Jackson Co., Texas, *Towner 175* (DS), this was a population of *C. serrulatus* which was only 2.2 mi E of a colony of *C. berlandieri* subsp. *berlandieri* (*Towner 176*), the two being identical except for pollen counts and the longer style lengths in the latter population.

Sympatry of *C. serrulatus* with members of sect. *Salpingia* is frequent. In the southern Great Plains, *C. hartwegii* subsp. *fendleri* is often found near or adjacent to populations of this species. Less commonly, *C. hartwegii* subsp. *pubescens* and *C. lavandulifolius* occur with *C. serrulatus* in the same region and at the eastern base of the Rocky Mountains. Lastly, in eastern and southeastern New Mexico, *C. hartwegii* subsp. *filifolius* occasionally comes in contact with *C. serrulatus* on calcareous plains east of the Pecos River. In none of these cases has any evidence of introgression or hybridization been observed.

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—subsp. strigulosus 50*, 58*, 60*, 75*, 89*, 91*, 96*–97*, **98**, 99*
—subsp. tubicula 58*, 60*, 63*, 75*, 89*, 91*, 95*, **96**, 97*, 99*, 110*
Camissonia 59*
Celerio
lineata 61*, 70*
Cercocarpus 88*
Clarkia 49*, 59*
amoena 51*
—subsp. amoena 51*
unguiculata 51*
Dialictus 87*, 95*, 110*, 116*
Evylaeus 77*, 83*, 87*, 95*, 106*, 110*, 116*
galpinsia 83*
Galpinsia 49*, **67**, **68**
camporum **84**
carlsbadiana **96**, 98*
fendleri **81**
filifolia **78**
glandulfera **96**
greggii **84**
hartwegi
—var. *fendleri* **81**
hartwegii 67*, **71**

interior **84**
lampasana **84**
lavandulaefolia **88**
—var. *glandulosa* **88**
toumeyi **92**
tubicula **96**
Gaura 49*, 51*, 59*, 65*, 116*
Gayophytum 59*
Halictus 110*
Hyles
lineata 61*, 69*, 87*, 91*, 95*, 106*
Hauya 49*
Heterogaura 49*
Juniperus 78*, 82*, 85*, 88*
Larrea
divaricata 76*, 78*, 88*, 96*
Lasioglossum 93*
Manduca 91*
quinquemaculata 87*
Megachile 87*, 110*
Melissodes 87*, 106*
Meriolix 49*, **67**, **99**
berlandieri **103**
capillifolia **107**
drummondiana **110**
hillii **107**, 109*
intermedia **111**
melanoglottis **107**, 109*
oblanceolata **111**
serrulata 67*, **110**
—var. *douglasii* **110**
—var. *drummondii* **110**
—var. *nuttallii* **110**
—var. *pinifolia* **107**
—var. *spinulosa* **110**
spinulosa **110**
Onagraceae 48*, 59*, 62*, 66*
—tribe Onagreae 48*, 49*
Oenothera 48*–51*, 59*, 116*
—subg. *Salpingia* 49*, 67*, **68**
—subg. *Calylophus* **99**
berlandieri **103**
camporum **84**
capillifolia **107**
fendleri **81**
greggii **84**, 86*, 87*
—var. *lampasana* **84**
—var. *pubescens* **84**
—var. *pringlei* 71*, 74*, **75**
—var. *typica* **84**
hartwegi
—var. *fendleri*
—subvar. *lavandulaefolia* **88**
—var. *tubicula* **96**
hartwegii **68**, 79*, 83*
—var. *fendleri* **81**
—subvar. *filifolia* **78**
—f. *thymifolia* **84**
—var. *filifolia* **78**
—var. *hartwegii* **71**, **78**, **81**, 83*
—var. *lavandulaefolia* **88**
—var. *toumeyi* **92**
—var. *typica* **71**, 74*, **78**, **81**, **88**
hookeri 59*
lampasana **84**
lavandulaefolia 67*, 74*, **88**
—var. *glandulosa* **88**, 91*
—var. *typica* **71**
lavandulifolia
—var. *lavandulifolia* **71**, 74*, **88**
leucocarpa **110**
pringlei **71**, **75**
serrulata 105*, **110**
—subsp. *drummondii* **103**, **107**, 108*, **110**
—subsp. *pinifolia* **103**, 105*, **107**
—subsp. *serrulata* **103**, **110**
—var. *douglasii* **110**
—var. *drummondii* **103**, **107**, **110**
—f. *flava* **107**, 108*, **111**
—var. *integrifolia* **111**
—var. *maculata* **107**
—var. *nuttallii* **110**
—var. *pinifolia* **103**, 105*, **107**
—var. *spinulosa* **110**
—var. *typica* **103**, **110**
× *serrulatoides* **96**
spachiana **110**
toumeyi **92**
tubicula **94**
—var. *demissa* **96**
—var. *filifolia* **78**
Opuntia 76*, 103*
Pinus
edulis 82*
monophylla **88**
ponderosa 82*, 88*
Prosopis 103*
glandulosa 76*, 82*, 85*
Quercus
havardii 103*
Salpingia **67**, **68**
hartwegii **71**
Sphecodogastra 83*
Sphinx
dolli 87*
Xylocopa 110*
Yucca 76*, 78*, 96*

CHROMOSOME NUMBERS IN LEGUMES[1]

Peter Goldblatt[2] and G. Davidse[3]

Abstract

Chromosome numbers are reported for 39 species representing 35 genera. The following are new generic (and specific) reports: *Acrocarpus fraxinifolius* $2n = 24$, *Amblygonocarpus andongensis* $2n = 28$, *Baikiaea plurijuga* $2n = 24$, *Brasilletia mollis* $2n = 24$, *Kotschya aeschynomenoides* $2n = 40$, *K. africana* $2n = 30$, *K. strigosa* $2n =$ ca. 36, *Maackia amurensis* $2n =$ (18)20, *Paramacrolobium coeruleum* $2n = 24$, *Schizolobium parahybum* $2n = 26$, *Sphaerophysa salsula* $2n = 16$, *Sphenostylis marginata* $2n = 22$, *Strongylodon macrobotrys* $2n = 28$, *Tachigalia paniculata* $2n = 26$, *Tylosema fassoglensis* $2n = 52$, *Xanthocercis zambeziaca* $2n = 26$, and *Virgilia oroboides* $2n =$ ca. 54. New species reports are the following: *Cordyla africana* $2n = 20$, *Desmodium barclayi* $2n = 22$, *Dioclea virgata* $2n = 22$, *Entada pursaetha* $2n = 28$, *Erythrina livingstoneana* $2n = 42$, *Mucuna sloanei* $2n = 22$, and *Sindora wallichii* $2n = 24$.

This paper is preliminary to a general review (P. H. Raven & P. Goldblatt, in preparation) of cytology in the Leguminosae. This work is being undertaken in conjunction with other systematic research in the family to be presented at the Legume Conference planned for 1978. The majority of counts reported here are for species and genera selected to fill some of the many gaps in the cytology of the family. Although there are a large number of chromosome counts in the Leguminosae, the family can still be said to be in general poorly known cytologically with an estimated 18% of the ca. 18,000 species having been investigated (Bandel, 1975). The present paper includes chromosome counts for 39 species in 35 genera. Of these, 15 are first reports for genera.

Materials and Methods

Root tips only were used in this study, hence all counts are mitotic. Root tips were pretreated either in cold water for 24 hours and stained using the Feulgen technique or were placed in 0.003 M hydroxyquinoline for 4–5 hours and stained in lactopropionic orcein. Species studied are listed in Table 1 and almost all plants have herbarium vouchers which are housed mainly at Missouri Botanical Garden (MO), but also at New York Botanical Garden (NY) or elsewhere.

Discussion

The results are listed in Table 1 and are discussed by subfamily and tribe. The three traditional subfamilies Papilionoideae, Caesalpinioideae, and Mimo-

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soideae are recognized. Tribal subdivisions are those of Hutchinson (1964) for Mimosoideae and Papilionoideae, while Taubert's (1891–1894) treatment is used for Caesalpinioideae as presented recently by Heywood (1971). Previously published chromosome numbers referred to in this paper are taken from the standard chromosome indices, particularly Darlington & Wylie (1955), Fedorov (1969), and the annual *Index to Plant Chromosome Numbers*, the most recent of which summarizes reports for 1972 (Moore, 1974).

MIMOSOIDEAE

Adenanthereae.—The report of $2n = 28$ in *Amblygonocarpus* is a new generic record. This count accords with $n = 14$ in *Prosopis* and other allied genera in the tribe where $x = 14$ is probably basic. Low base numbers of $x = 13$ in *Adenanthera*, *Piptadenia*, *Neptunia*, and others, and $x = 12$ in *Calpocalyx* and *Xylia* are most likely derived. The count for *Entada purseatha* is a new species record and in accord with $n = 14$ reported for several other species of this genus.

Ingeae.—The count of $2n = 26$ for *Samanea saman* confirms a previous record for this species. A base number of $x = 13$ has been reported in several genera of the tribe with the only exception, *Calliandra*, $x = 8$, standing out here. Counts for more genera in this tribe are needed before the significance of the exceptional $x = 8$ can be assessed.

CAESALPINIOIDEAE

Caesalpinieae.—Counts in this group for *Caesalpinia pulcherrima* ($2n = 24$) and *Delonix regia* ($2n = 28$) confirm previous reports for these species. Counts for *Acrocarpus* ($2n = 24$), *Schizolobium* ($2n = 26$), and *Brasilettia* ($2n = 24$) are new generic records. With $x = 14$ probably basic in this alliance and with $x = 12$ and 11 well established in several other genera, present counts are consistent with the cytological pattern of this tribe. The number $2n = 26$ in *Schizolobium* is, however, a new number for Caesalpinieae.

Detarieae.—The counts for *Baikiaea*, $2n = 24$, and *Tachigalia*, $2n = 26$, are new generic records. The number in *Baikiaea* is consistent with the majority of chromosome numbers in Detarieae where $x = 12$ is probably basic. Other numbers in the tribe are $n = 10$ and $n = 8$ reported in only a few genera. The record of $2n = 26$ for *Tachigalia paniculata* is a new number for the tribe.

The count for *Sindora wallichii* is a first report for this species. Other counts in *Sindora* are $n = 12$ in *S. siamensis*, $n = 10$–12 in *S. cochinchinensis*, and $n = 8$ in *S. supa*. Unless *Sindora* is cytologically heteroploid, $n = 12$ would seem most likely correct for the genus. *Sindora supa* should, however, be checked to verify the unusual $n = 8$ reported by Atchison (1951).

The count of $2n = 24$ for *Afzelia africana* confirms previous reports for this species.

Amherstieae.—The report for *Paramacrolobium* is a new generic record and the number $2n = 24$ is consistent with $x = 12$ in the seven other genera of Amherstieae known cytologically.

Cerceae.—The count for *Tylosema fassoglensis*, a segregate of *Bauhinia* (al-

TABLE 1. Chromosome numbers of Leguminosae. Entries preceded by one asterisk (*) are the first report for that species; entries preceded by two asterisks (**) are the first report for that genus.

Species	Chromosome Number 2n	Collection and Voucher Information
	MIMOSOIDEAE	
	Adenanthereae	
***Amblygonocarpus andongensis* (Welw. ex Oliv.) Exell & Torre	28	Rhodesia, Victoria Falls Station, *Gordon s.n.* (no voucher).
**Entada pursaetha* DC.	28	Ghana, Eastern Region, Nyanao Hill, *Faden et al.* 74/72 (MO).
	Ingeae	
Samanea saman (Jacq.) Merr.	26	Ghana, Eastern Region, Achimota, *Faden & Faden 74/80* (MO).
	CAESALPINIOIDEAE	
	Caesalpinieae	
***Acrocarpus fraxinifolius* Wight & Arn.	24	Kenya, Kiambu Distr., Thika, (cultivated). *Faden et al. 74/1314.*
***Brasilettia mollis* (H.B.K.) Britton & Killip	24	Venezuela, Guárico, near Valle de la Pascua, *Davidse 4497* (MO).
Caesalpinia pulcherrima (L.) Swartz	24	Virgin Islands, St. Croix, *Nelson s.n.* (MO).
Delonix regia (Hook.) Raf.	28	Ghana, Eastern Region, Achimota, *Faden et al. 74/79* (MO).
***Schizolobium parahybum* (Vell.) Blake	26	Brazil, Para, Belem *Murça Pires 75/4* (NY).
	Detarieae	
Afzelia africana Smith	24	Ghana, Eastern Region, Achimota, *Faden et al. 74/54* (MO).
***Baikiaea plurijuga* Harms	24	Rhodesia, Lupane Distr., near Amandundumela River, *Forest Officer s.n.* (NY).
**Sindora wallichii* Benth.	24	Singapore Botanic Garden, cultivated, *Ahmad SA1297* (MO).
***Tachigalia paniculata* Aubl.	26	Colombia, Chocó, Serrania del Darién, *Gentry 15276* (MO).
	Amherstieae	
***Paramacrolobium coeruleum* (Taub.) Léonard	24	Kenya, Kwale Distr., Buda Forest, *Faden & Faden 74/319* (MO).
	Cerceae	
Piliostigma thonningii (Schum.) Milne-Redhead	24	Kenya, Muraga Distr. near Fort Hall, *Davidse 6996* (MO).
***Tylosema fassoglensis* (Kotschy) Torre & Hillcoat	52	Malawi, Northern Prov., near Chilumba, *Pawek 9554A* (MO).

TABLE 1. (continued)

Species	Chromosome Number 2n	Collection and Voucher Information
	FABOIDEAE/PAPILIONOIDEAE	
	Swartzieae	
**Cordyla africana* Lour.	20	Kenya, Kwale Distr., Marenje Forest, *Faden & Faden 74/319* (MO).
	Sophoreae	
***Maackia amurensis* Rupr. & Maxim.	(18)20	Cult. Arnold Arboretum, *Palmer s.n.* (A). (Native of China, original source not known.)
Sophora tomentosa L.	18	Brazil, Santa Catarina, Itajai *Conrad & Dietrich 2139* (MO).
	18	Kenya, Kwale Distr., Diani Beach, *Faden & Faden 74/315* (MO).
***Virgilia oroboides* (Berg.) Salter	ca. 54	South Africa, Cape Bettys Bay, *Ebersohn s.n.* (NBG).
***Xanthocercis zambeziaca* (Baker) Dumaz le Grand	26	South Africa, Transvaal, Tchipse Holiday Camp, *Nel 330* (NBG).
	Podalyrieae	
Chorizema cordatum Lindl.	16	Australia, wild source not known, *Wittunga Botanic Garden 3464* (AD).
Daviesia latifolia R. Br.	18	Australia, Tasmania, Mt. Wellington, *Ratkowsky 774* (MO).
Gompholobium huegellii Benth.	18	Australia, Tasmania, Boronia Hill, Hobart, *Ratkowsky s.n.* (MO).
Viminaria juncea (Schrad.) Hoffmg.	18	Australia, Victoria, Grampiens, *Trezize s.n.* (AD-5623).
	Tephrosieae	
Mundulea sericea (Willd.) A. Chev.	22	South Africa, Transvaal, Hectorspruit, *Nel s.n.* (NBG).
	Sesbanieae	
Sesbania seseban (L.) Merr. var. *nubica* Chiov.	12	Kenya, Nakuru Distr., Lake Nakuru Natl. Park, *Davidse 7098* (MO).
	Coluteae	
***Sphaerophysa salsula* (Pall.) DC.	16	USA, Nevada, Churchill Co., *Martinelli & Fuller 20109* (MO).

TABLE 1. (continued)

Species	Chromosome Number 2*n*	Collection and Voucher Information
	Diocleae	
**Dioclea virgata* (Rich.) Amshoff	22	Brazil, Para, Belem, (no voucher).
Canavalia maritima L.	22	Virgin Islands, St. Croix, *Nelson 7* (MO).
	Erythrineae	
Erythrina amazonica Krukoff	84	Brazil, Maranhão, Lapela, *Silva 4238* (NY).
**E. livingstoneana* Baker	42	Rhodesia, near Triangle, *Müller s.n.* (no voucher).
**Mucuna sloanei* Fawc. & Rendle	22	Ghana, Eastern Region, SW of Adaiso, *Faden et al. 74/57* (MO).
M. pruriens var. *utilis* (Wright) Burk	22	Ghana, Eastern Region, Achimota, *Faden et al 74/78* (MO).
***Strongylodon macrobotrys* A. Gray	28	Cult. Longwood Gardens, (no voucher) (origin unknown).
	Phaseoleae	
***Sphenostylis marginata* E. Mey.	22	Malawi, Northern Prov. Mzuzu, Marymount, *Pawek 10408* (MO).
	Aeschynomeneae	
***Kotschya africana* Endl.	30	Malawi, Northern Prov., Nyika Plateau, *Pawek 10013* (MO).
***K. strigosa* de Wit & Duvign.	ca. 36	Malawi, Northern Prov., Mzuzu, Marymount, *Pawek 5541* (MO).
***K. aeschynomenoides* (Baker) de Wit & Duvign.	40	Malawi, Northern Prov., Nyika Plateau, *Pawek 10019* (MO).
	Desmodieae	
**Desmodium barclayi* Benth.	22	Panama, Canal Zone, Farfan Beach, *Dwyer 11963* (MO).

though included in *Bauhinia* by some authors), is a new generic record. This species appears to be tetraploid with a base number of $x = 13$. The number reported here supports the exclusion of *T. fassoglensis* from *Bauhinia* in which $x = 14$ is clearly basic and only multiples of this have been recorded in the genus. In the other relative of *Bauhinia* studied here, *Piliostigma thonningii*, we have obtained $2n = 24$, which supports an earlier report by Mangenot & Mangenot (1962) and conflicts with Turner & Fearing's (1959) report of $2n = 26$ for this species. The other species of *Piliostigma* known cytologically have $2n = 28$ (Miège, 1960; Sharma & Raju, 1966), a number indicating closer affinity with *Bauhinia* perhaps than with *P. thonningii*.

PAPILIONOIDEAE

Swartzieae.—The count of $2n = 20$ in *Cordyla africana* is a new species record and supports a previous count in this genus. Only two of the nine genera in Swartzieae are known cytologically, the other being *Swartzia* with $n = 8$.

Sophoreae.—Reports for *Maackia*, *Virgilia*, and *Xanthocercis* represent new generic records, while $2n = 18$ for *Sophora tomentosa* confirms several previous counts for this species. Although $n = 9$ is the most frequent number in Sophoreae, $x = 14$, $x = 13$, $x = 11$, $x = 10$, and $x = 8$ are other base numbers that have also been reported in several genera. With this range of chromosome numbers, the counts of $n = (9)10$ in *Maackia* and $n = 13$ in *Xanthocercis* appear consistent with the present circumscription of the tribe. The number in *Maackia* could not be more firmly established, and the possibility exists that a small pair of chromosomes may represent large satellites. Given the frequency of $n = 9$ in Sophoreae, $2n =$ ca. 54 in *Virgilia oroboides* appears to indicate hexaploidy in this species and a base number of $x = 9$ for the genus.

Podalyrieae.—Counts for the four Australian species studied here support recent detailed cytological work for the Australian species of this tribe (Sands, 1975). Important numbers in Podalyrieae are $n = 9$ and 8 with a few genera also $n = 7$. As pointed out by Polhill (1976), $n = 9$ occurs in the South African and north temperate Podalyrieae, while $n = 9$, as well as $n = 8$ and 7, occur in the Australian representatives of the tribe.

Tephrosieae.—The count for *Mundulea sericea* confirms previous records for this species in which both $n = 10$ and 11 have been reported. This suggests that the count of $n = 10$ may be erroneous, particularly as $x = 11$ also occurs in the majority of species of the related genus *Tephrosia*. Lower counts of $n = 8$ in *Tephrosia* (Sands, 1975) and $n = 8$ in the related *Sphinctospermum* may be correlated with the advanced position of these species.

Sesbanieae.—The report of $2n = 12$ in *Sesbania sesban* confirms earlier counts for this species and is consistent with numerous reports of $n = 6$ in *Sesbania*. The only other reports in the tribe are $n = 8$ for *Cracca*, which should in fact be excluded from Sesbanieae according to R. M. Polhill (personal communication).

Coluteae.—The count of $2n = 16$ in *Sphaerophysa* is a first report for this genus. All other genera of this tribe, widespread in the Old World, that are known cytologically have $x = 8$, presumably basic for the alliance.

Diocleae.—The report of $2n = 22$ for *Dioclea virgata* is a new species report, while that for *Canavalia maritima* confirms a previous count for this species. Previous counts for *Dioclea* are $2n = 22$ in *D. reflexa* (Mangenot & Mangenot, 1958, 1962) and $2n = 24$ in *D. boykinii* (Němec, 1910). Our second report of $2n = 22$ in *Dioclea* throws some doubt on Němec's record, especially as $x = 11$ is clearly basic in *Camptosema*, *Canavalia*, and *Pueraria*, the only other genera of Diocleae for which chromosome numbers are known.

Erythrineae.—The count of $2n = 42$ for *Erythrina livingstoneana* is a first record for this species, while the count of $2n = 84$ for *E. amazonica* confirms previous reports of tetraploidy in this species, $n = 21$ being basic in *Erythrina*.

Counts of $2n = 22$ in *Mucuna* confirm previous reports in the genus, the record for *M. sloanei* being new for this species. The report for *Strongylodon* is a new generic record and a new chromosome number for this tribe which is cytologically heterogeneous with numbers ranging from $x = 21$, $x = 14$, $x = 11$, and $x = 9$ (and possibly also $x = 10$).

Phaseoleae.—The count of $2n = 22$ in *Sphenostylis* is a first record for this genus. The number accords well with other reports for the tribe, the majority of genera known cytologically having $n = 11$. Only a few genera stand out as different, notably *Endomallus* with $x = 8$ and *Psophocarpus* where $n = 11$, 10, and 9 are reported. There are also a few reports of $n = 10$ in *Vigna* and *Dolichos* which require investigation since they differ from $n = 11$ in most species of both genera.

Aeschynomeneae.—Counts reported here for three species of *Kotschya* represent the first cytological records for this genus. Other counts in the tribe are $n = 10$ in *Aeschynomene* and *Brya*, $n = 12$ (probably) in *Ormocarpum*, and $n = 19$ (again probably) in *Smithia*. *Kotschya* does not appear to conform with the previously reported numbers for *Aeschynomene*, the three species reported here having $n = 15$, $n =$ ca. 18, and $n = 20$, respectively. More counts in *Kotschya* and in the tribe are needed to clarify the cytology of this alliance.

Desmodieae.—The count for *Desmodium barclayi* is the first report for this species and is consistent with $n = 11$, the only reported number in *Desmodium*.

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FOUR SPECIES OF ASCLEPIADACEAE NEW TO PANAMA

David L. Spellman[1]

Abstract

Fischeria brachycalyx, *Gonolobus rothschuhii*, *Matelea pseudobarbata*, and *M. viridis* are newly reported for the Panamanian flora. *Matelea viridis* (Moldenke) Spellman is a new combination based on *Fischeria viridis* Moldenke.

Recent collections of plants from poorly known areas of Veraguas and Darién Provinces in Panama have added three species of Asclepiadaceae to the flora of the country. Further studies of the family have resulted in a new combination for one of the three, as well as the addition of a fourth species to the flora which was incorrectly assigned in the treatment of the family for the *Flora of Panama* (Spellman, 1975).

1. **Fischeria brachycalyx** L. O. Williams, Fieldiana: Bot. 32: 43. 1968. TYPE: Costa Rica, *Austin Smith 1211* (F, GH, MO, NY).

Stems glandular puberulent and hispid, the longest trichomes brown, to 3 mm long. *Leaves* elliptic, apically acuminate, basally cordate, mostly 9–12 cm long, 4–6 cm wide, the upper surface scabrous, the lower surface softly hispid; petioles glandular puberulent and hispid, mostly 3–5 cm long. *Inflorescences* racemose, glandular puberulent and hispid-pilose throughout; peduncles 4.5–8 cm long, pedicels 3–4 cm long. *Flowers* 1.4–2 cm in diameter; calyx abaxially glandular puberulent and hispid-pilose, adaxially glabrous or nearly so, the lobes lance-ovate, 4.7–7 mm long, 1.5–2.5 mm wide; corolla light green, shallowly campanulate, the lobes ovate, 6–7 mm long, 3.5–5.5 mm wide, strongly crispate near the apex on one margin, the upper surface papillate in a median band, this overtopped by long white trichomes of variable density, the lower surface appressed brown pubescent, the crispate margin ciliate; gynostegium 2–2.5 mm high, inflated portions of the anthers suborbicular in surface outline; corona prominently 5-gonal to shallowly lobate, the surface striate-sulcate. *Follicles* obliquely ellipsoid, 19–24 cm long, ca. 3–4 cm in diameter, the walls thick, sublignose, finely striate, drying reticulate, sparsely pubescent; seeds compressed-ovate, 10–12 mm long, 6.5–7 mm wide, the marginal wing irregularly and deeply toothed apically (fruit described from Costa Rican material).

Occurring in partial shade of moist forest, this species is most frequently collected at elevations from 1,000 to 1,400 m in Costa Rica and Panama.

Using the keys given in the *Flora of Panama*, this species is identified as *Fischeria columbiana* Schlechter. The latter species is readily separated from *F. brachycalyx* in having its pedicels and calyces puberulent but lacking longer hispid trichomes. In addition, the surface of the corona of *F. columbiana* is vermiform-fimbriate rather than striate-sulcate.

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Ann. Missouri Bot. Gard. 64: 129–132. 1977.

VERAGUAS: Río Primero Braso, 2.5 km beyond Agriculture School, Alto Piedra near Santa Fé, 700–750 m, 24 July 1974, *Croat 25533* (MO).

2. **Matelea viridis** (Moldenke) Spellman, comb. nov.

Fischeria viridis Moldenke, Phytologia 1: 13. 1933. TYPE: Colombia, *A. E. Lawrance 396* (F, GH, K, MO).

Stems densely glandular puberulent and sparsely pilose. *Leaves* elliptic to slightly obovate, apically rounded and abruptly acuminate, the upper surface softly scabrous, the lower surface hirsute; blades 8–12 cm long, 3–4 cm wide; petioles glandular puberulent and pilose, 1–1.5 cm long. *Inflorescences* racemose, densely brown, glandular puberulent and pilose throughout; peduncles 3.5–4.5 cm long; pedicels 2.5–3 cm long. *Flowers* 2.5–3 cm in diameter; calyx densely glandular puberulent and pilose abaxially, glabrous adaxially, the lobes lanceolate, 4.3–4.7 mm long, 1.3–1.5 mm wide, reflexed at anthesis; corolla greenish white with darker green reticulate "veins," shallowly campanulate-rotate, deeply lobed, the lobes lance-ovate but folded lengthwise to appear ligular, 10.4–11 mm long, 5.5–6 mm wide, undulate-crispate on one or usually both margins, the upper surface glabrous except for a dense median band of minute papillae, the lower surface puberulent; gynostegium 3–3.5 mm high, yellow green and white; corona carnose, sharply 5-lobed, the lobes triangular, the surfaces colliculate, the corona column smooth and appendaged, the appendages ± ligular, situated above each lobe, curving up around the gynostegium-head. *Follicles* ellipsoid, attenuate to the apex, smooth, glabrous, to 19.5 cm long, ca. 4.5 cm in diameter; seeds spatulate, 8.6–9.3 mm long, 4.7–5 mm wide, the marginal wing coarsely serrate in the apical half.

The collection cited below represents the third known collection of this species. The other two localities are from the central cordillera of Colombia at elevations from 1,200 to 2,000 m.

The species is excluded from *Fischeria* primarily on the basis of its lack of dorsally inflated anthers. It differs also in the more technical aspects of its pollinia and gynostegium morphology.

In the keys to the family given in the *Flora of Panama*, *M. viridis* cannot be placed in the proper genus. With some effort, it can be forced through the keys to *Fischeria*. It differs from other species of *Matelea* in its ligular-appearing, undulate-crispate corolla lobes.

VERAGUAS: Lower montane wet forest 6–7 km W of Santa Fé on new road past Agricultural School, 2,900 ft, 17 Feb. 1974, *Nee 9791* (MO).

3. **Matelea pseudobarbata** (Pittier) Woods., Ann. Missouri Bot. Gard. 28: 235. 1941.

Gonolobus pseudobarbatus Pittier, Contr. U.S. Natl. Herb. 13: 105. 1910. TYPE: Costa Rica, *Brenes s.n.* (K, US).

Slender *vines*. Brown, glandular puberulent throughout, stems, petioles, and inflorescences also with hispid-pilose hairs to 3 mm long. *Leaves* ovate, apically tapering, basally cordate, 6.5–8.5 cm long, 3.5–4.5 cm wide, the basal sinus nar-

row, 1–1.5 cm deep, the upper surface puberulent with scattered hispid-pilose hairs, the lower surface glandular puberulent, the veins and veinlets becoming conspicuously dark upon drying; petioles 2.5–3 cm long. *Inflorescences* condensed racemes, appearing ± umbelliform, ca. 10–15-flowered, but with the flowers opening in pairs; peduncles 2.8–3 cm long; pedicels 1.2–1.7 cm long. *Flowers* ca. 1 cm long at anthesis; calyx densely glandular puberulent and pilose abaxially, glabrous adaxially, the lobes lanceolate to ovate-acuminate, 2.5–3 mm long, 1–1.6 mm wide; corolla ca. 1.2 cm in diameter when extended, rotate but the lobes sharply reflexed at anthesis, the tube 0.6–0.7 mm long, the lobes elliptic to ovate, obtuse, 4.7–5 mm long, 3.3–3.7 mm wide, the upper surface villous-pilose, rarely glabrous or nearly so, the trichomes ca. 1.5 mm long, the lower surface glandular puberulent except at the base of the lobes and near the margins, the margins ciliate with cilia 1–2 mm long; corona annular, purple black, carnose, ca. 1 mm high, the surface bullate-colliculate; gynostegium slightly exceeding the corona, the head obscurely 5-gonal. *Follicles* (from Costa Rican material) said to be ellipsoid-attenuate, dark olive green, shiny, armed with soft, blunt-tipped spines or tubercles, the immature follicles 16.5 cm long.

Matelea pseudobarbata is known from elevations of 1,000 to 2,000 m in Costa Rica.

This species is closely related to, and was mistakenly reported as, *M. pinguifolia* (Standley) Woods. in the *Flora of Panama*, a species strictly limited to the lowlands. The rounded cordate leaves with inconspicuous veins and lack of long trichomes in the inflorescence characterize *M. pinguifolia* and clearly separate it from *M. pseudobarbata*.

CHIRIQUÍ: At opening to canyon to Bambito, 5,000 ft, 28 June 1969, *Tyson 5860* (DUKE, FSU, MO).

4. **Gonolobus rothschuhii** Schlechter, Bot. Jahrb. Syst. 60: 368. 1926. TYPE: Nicaragua, *Rothschuh 557* (B, destroyed, photo MO).

Fischeria heterophylla Hemsl., Biol. Centr. Amer., Bot. 2: 230. 1881. TYPE: Nicaragua, *Tate 171 (240)* (K).

Stems puberulent and hispid-pilose, the longest trichomes to 3 mm long. *Leaves* elliptic, apically rounded and abruptly acuminate, basally truncate to shallowly cordate, mostly 12–15 cm long, 5.5–7 cm wide, the upper surface strigose with hairs 1.5–2 mm long, the lower surface sparsely hirsute; petioles puberulent and pilose, 2–3 cm long. *Inflorescences* contracted racemes, apparently ca. 10-flowered but with usually no more than 2 open at one time; peduncles 3–5 mm long, sparsely hispid-pilose; pedicels 18–21 mm long, hispid-pilose. *Flowers* 2.5–3 cm in diameter; calyx abaxially pilose, adaxially glabrous but for a median line of pilose trichomes, the lobes linear-lanceolate, sharply reflexed at anthesis, mostly ca. 8.5 mm long, 0.9–1.5 mm wide; corolla green becoming greenish bronze, rotate, deeply cut, the lobes linear-lanceolate, mostly 14 mm long, 3–3.5 mm wide, the upper surface glabrous, the lower surface pilose; gynostegium 1.4–1.7 mm high, the anther appendages cuneate, bilobed, the lobes diverging to form a concave triangle, ca. 1 mm long, 1.5 mm wide, the lobes

curling in drying; faucal annulus only slightly raised and somewhat fleshy, nearly obscured by the corona; corona remotely 5-gonal, fleshy, the margins thickened, rugose; ovaries 3-ridged, glabrous. *Follicles* unknown.

This species is typically found at elevations from 1,200 to 1,800 m in Costa Rica, Honduras, Nicaragua, and possibly Guatemala.

A distinctive species, *Gonolobus rothschuhii* is separated from all other Panamanian members of the genus by its very narrow corolla lobes and color, and by the shape of its anther appendages.

DARIÉN: Cerro Tacarcuna, south slope, ridge-top forest well below summit, premontane wet forest, 1,250–1,450 m, 26 Jan. 1975, *Gentry & Mori 13921* (MO).

Literature Cited

SPELLMAN, D. L. 1975. Asclepiadaceae. *In* R. E. Woodson, Jr. & R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 62: 103–156.

NEW SPECIES OF *GIBSONIOTHAMNUS* (SCROPHULARIACEAE/BIGNONIACEAE) AND *TOURNEFORTIA* (BORAGINACEAE) FROM EASTERN PANAMA AND THE CHOCÓ[1]

ALWYN H. GENTRY[2]

ABSTRACT

Three new species are described from wet forest regions of eastern Panama and the Chocó of Colombia—*Gibsoniothamnus alatus* A. Gentry, *Gibsoniothamnus mirificus* A. Gentry, and *Tournefortia tacarcunensis* A. Gentry & Nowicke.

Gibsoniothamnus alatus A. Gentry, sp. nov.

Frutex epiphyticus. Ramuli irregulariter teretes. Folia elliptica, acuta vel acuminata, cuneata, glabra praeter domatia ciliata. Flores singulares, pedicellis glabris. Calyx late alatus, ad instar stellae, alis ultra 1 cm longis. Corolla (non vidi) alba.

Epiphytic shrub. Branchlets irregularly terete to subangulate, very sparsely pilose. Leaves elliptic, acute to acuminate, cuneate at the base, chartaceous to subcoriaceous, glabrous above and below except for ciliate domatia in the axils of the lower secondary nerves, gland dotted below, the margin entire, very slightly or not at all revolute, drying dark olive above, light olive below, the secondary veins plane or slightly impressed above, prominulous to prominent below. Inflorescence a single flower; pedicel glabrous, 1.5–2 cm long. Calyx very broadly winged, glabrous except a few trichomes near the ends of the wings, almost star shaped, ca. 6–7 mm long and wide without the wings, the wings each over 1 cm long, tapering to an acute point. Corolla (not seen) white. Pistil 23 mm long, the ovary globose, the style slender, 18 mm long. Fruit white, covered by the calyx.

TYPE: PANAMA. DARIÉN: N slopes of Cerro Pirre, lower montane rain forest (cloud forest), 700–950 m, 6 Apr. 1975, *Mori & Kallunki 5449* (MO, holotype; isotypes to be distributed).

Additional collection examined: PANAMA. DARIÉN: Cerro Campamento, S of Cerro Pirre, elfin forest, 20–22 Mar. 1968, *Duke 15657* (MO).

This species is utterly distinct in the genus because of its laterally winged, star-shaped calyx. Its closest relative is *G. pterocalyx* A. Gentry but that species has much narrower longitudinally oriented teeth.

Gibsoniothamnus mirificus A. Gentry, sp. nov.

Frutex epiphyticus. Ramuli irregulariter subangulati, pilosi. Folia obovato-elliptica, obtusa, cuneata, conspicue pilosa. Flores singulares, pedicellis pilosis. Calyx cupulatus, pilosus, valde 5-dentatus, dentibus linearibus, 2–2.5 cm longis. Corolla tubulosa, rubra.

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Epiphytic shrub. Branchlets pilose, irregularly subangulate. Leaves obovate-elliptic, obtuse to acutish at the apex, cuneate at the base, chartaceous to subcoriaceous, 3–9 cm long, 1.5–4 cm wide, conspicuously pilose with 1–2-mm-long trichomes above and below, the margin entire, very slightly or not at all revolute, drying brownish olive above, tannish yellow below, the secondary veins plane above, prominent below; petiole densely pilose, ca. 5 mm long. Inflorescence a single flower; pedicel conspicuously pilose, 0.7–1 cm long. Calyx cupular, pilose, strikingly 5-toothed, 5–7 mm long and 4–6 mm wide without the teeth, the 5 linear teeth exceeding the calyx by 2–2.5 cm, pilose, extended along the calyx as lateral ridges. Corolla red, tubular, glabrous, 3.5–4.3 cm long and 0.5–0.6 cm wide, lobes 3 mm long, with ciliate margins. Fruits not seen.

TYPE: PANAMA. COLÓN: Santa Rita Ridge Road along trail from end of road (10.6 km from Transisthmian Highway, 3 km beyond hydrographic station) to Río Indio, 380 m, 13 Apr. 1976, *Croat 34298* (MO, holotype; PMA, isotype).

Additional collection examined: PANAMA. COLÓN: Plant collected by H. Wiehler on Santa Rita Ridge, cultivated at Marie Selby Botanical Gardens, Sarasota, Florida, *Dressler s.n.* (MO).

The striking calyx teeth of this species are by far the longest in the genus. It is otherwise similar to Costa Rican *G. epiphyticus* (Standl.) L. Wms. which is also more or less pilose throughout but has very much shorter calyx teeth, a fasciculate several-flowered inflorescence, and more coriaceous leaves.

Tournefortia tacarcunensis A. Gentry & Nowicke, sp. nov.

Herba erecta. Folia anguste elliptica, acuta, cuneata, subsessilia, glabrescentia. Inflorescentia scorpioidea, floribus sepalis lanceolatis, ca. 4 mm longis, corollae tubo 8–9 mm longo, lobis ca. 1.5 mm longis.

Herb 0.2–0.5 m; stems glabrescent. Leaves alternate, narrowly elliptic, acute, cuneate at the base, entire, with 4–7 pairs of strongly ascending secondary nerves, 8–28 cm long, 2–6.5 cm wide, glabrous above, glabrescent below, rather succulent when fresh, membranous when dry, drying dark brown above, tannish gray below; petiole essentially lacking. Inflorescence scorpioid, contracted, 3–4 cm long, terminal; pedicels mostly 1–2 mm long. Calyx of 5(6) free sepals, lanceolate, ca. 4 mm long, sparsely puberulous; corolla orangish to greenish cream, sparsely puberulous outside, the tube 8–9 mm long, the lobes ca. 1.5 mm long; stamens 5(6), borne near the apex of the corolla tube, sessile, the anthers ca. 1.2 mm long; ovary ovoid, the style ca. 6 mm long, the stigma conical, 1 mm long. Fruit not seen.

TYPE: PANAMA. DARIÉN: Cerro Tacarcuna, W ridge, trail from summit camp to waterfall E of camp, 1,550–1,700 m, lower montane wet forest life zone, herb 0.5 m, flowers greenish cream, turning tannish, inflorescence scorpioid, stamens equalling petal number, ovary 2-locular with axile placentation, 2 Feb. 1975, *Gentry & Mori 14114* (MO, holotype).

Additional collection examined: COLOMBIA. CHOCÓ: Slopes of Serranía del Darién, E of Unguía, premontane wet forest, ca. 1,300 m, herb 0.2 m, flowers orangish, 19 July 1976, *Gentry, León & Forero 16772* (COL, MO).

This species seems remarkably distinct from all other members of the genus. It is apparently the only clearly herbaceous species of *Tournefortia* (a completely unrelated species, *T. sibirica* L. is a wiry herb but often segregated as *Messerschmidia*). Another unusual feature is a tendency to 6-parted flowers.

The pollen of *T. tacarcunensis* is of the type described as "Type II," 3-colporate, subprolate with expanded poles, psilate at the poles and verrucate at the equator by Nowicke & Skvarla (1974).

The closest relative of *T. tacarcunensis* may be *T. ramonensis* Standl. of upland Costa Rica and Chiriquí Province—though omitted from the *Flora of Panama* treatment of the family (Nowicke, 1969). That species has generally similar flowers which differ in the corolla being densely and rather strigosely pubescent outside. The inflorescence of *T. ramonensis* is also much more elongate and the flowers are essentially sessile. Vegetatively *T. tacarcunensis* differs conspicuously in its glabrescent, narrowly elliptic leaves which are narrowly cuneate, essentially sessile, and have only about 6 pairs of secondary nerves. Another Costa Rican relative is *T. brenesii* Standl., which agrees in pedicellate flowers and an only sparsely puberulous corolla but has much longer (4 mm) corolla lobes and a long-petioled leaf with 15 secondary nerves on each side.

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NOTES

NEW COMBINATIONS IN *EPILOBIUM* (ONAGRACEAE)

In the course of preparation of a revision of the North American species of *Epilobium*, we have found the new combinations proposed in this paper to be desirable. They will be fully discussed and justified in our subsequent publications, but are offered at this time, with minimal synonymy, in order to make the names available.

Epilobium ciliatum Raf., Med. Repos. II. 5: 361. 1808.
Epilobium ciliatum subsp. **ciliatum**.

E. adenocaulon Hausskn., Oesterr. Bot. Z. 29: 119. 1879.
E. leptocarpum Hausskn. var. *macounii* Trel., Annual Rep. Missouri Bot. Gard. 2: 103. 1891.
E. brachycarpum sensu Munz, Aliso 4: 489. 1960; N. Amer. Fl., ser. 2, 5: 218. 1965, non Presl 1831.

Epilobium ciliatum subsp. **glandulosum** (Lehm.) Hoch & Raven, comb. nov. Based on *E. glandulosum* Lehm., Stirp. Pug. 2: 14. 1830.

E. boreale Hausskn., Monogr. Epil. 279. 1884.
E. exaltatum sensu auct. mult.; non Drew, Bull. Torrey Bot. Club 16: 151. 1889.

Epilobium ciliatum subsp. **watsonii** (Barbey) Hoch & Raven, comb. nov. Based on *E. watsonii* Barbey, in Brew. & S. Wats., Bot. Calif. 1: 219. 1876.

Epilobium hornemannii Reichenb., Icon. Crit. 2: 73, *fig. 313*. 1824.
Epilobium hornemannii subsp. **hornemannii**.
Epilobium hornemannii subsp. **behringianum** (Hausskn.) Hoch & Raven, comb. nov. Based on *E. behringianum* Hausskn., Monogr. Epil. 277. 1884.

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CHROMOSOME NUMBER IN *PILLANSIA* (IRIDACEAE)

The chromosome number in the South African monotypic genus *Pillansia* was previously reported (Goldblatt, 1971) as $2n = 44$. New material obtained subsequently proved without doubt to be $2n = 40$ (Fig. 1). The earlier record was obtained from paraffin sections of root tips and from anther squashes where 22 bivalents were noted. Plants in the earlier study were all from Rooi Els, Bettys Bay, Cape Prov., South Africa, [*Goldblatt 471* (BOL)], and those used in the present work were from Arieskraal, Cape Prov., South Africa, [*Powrie s.n.*

FIGURE 1. Metaphase chromosomes of *Pillansia templemanii* stained with lacto-propionic orcein; × 1,200.

(MO)] some distance away. A squash technique was used with the new material, and root tips were treated as described elsewhere (Goldblatt, 1976).

Pillansia is a monotypic genus of Iridaceae belonging to the exclusively Old World and predominantly African subfamily Ixioideae. The only species *P. templemanii* (Baker) L.Bolus is rare and occurs in a very localized area of the southwestern Cape Province of South Africa. Although it is undoubtedly a member of the Ixioideae, it is peculiar in this subfamily in several respects and hence of particular interest. Most remarkable is its paniculate inflorescence, quite unlike the spike, typical of the subfamily. The branched panicle is believed to be an ancestral condition from which the spike was derived, which suggests that *Pillansia* is a primitive Ixioid. A second peculiarity of *Pillansia* is that the corms are persistent, lasting several seasons instead of being annual as is usual in the Ixioideae. Lewis (1954) suggested that this condition in *Pillansia* was possibly transitional in the evolution of the corm from a rhizome. Thus *Pillansia*, primitive in both its inflorescence and rootstock, is probably a significant evolutionary link between the Ixoideae and less specialized subfamilies of Iridaceae, or their ancestors.

The chromosome number of $2n = 20$ reported here confirms the polyploid condition in the genus. The closest allies of *Pillansia*—*Watsonia*, *Thereianthus*, and *Micranthus* which together comprise subtribe Watsoniinae (Goldblatt 1971)—are in contrast basically diploid, with $x = 10$ in *Thereianthus* and *Micranthus* and $x = 9$ in *Watsonia*. As it is unlikely that *Pillansia* is heteroploid, the earlier report of $n = 22$ appears erroneous. Unfortunately, no more material is available at present to investigate the situation more fully.

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A NEW *JACARANDA* (BIGNONIACEAE) FROM ECUADOR AND PERU

Jacaranda sparrei A. Gentry, sp. nov.

Arbor. Folia pinnatim bicomposita, plerumque 13-pinnata, pinnis 13–21-foliolatis, foliolis 1–2 cm longis, 0.5–1 cm latis, apiculatis. Flor calyce fere patelliformi, 5-dentato, corolla tubulo-campanulata supra basim angustatam arcuatam, extus puberula, staminodio exserto, antheris 1-thecatis, ovario puberulo. Fructus ignotus.

Tree; branchlets subtetragonal, very minutely puberulous, with whitish lenticels. Leaves pinnately bicompound, usually with 13 pinnae, each pinna with a slightly winged rachis and 13–21 sessile, asymmetrically oblong leaflets, these 1–2 cm long and 0.5–1 cm wide, apiculate, glabrescent above, barbate at least along the base of midvein below. Inflorescence an open terminal panicle, puberulous. Flowers with the calyx almost patelliform, shallowly 5-dentate, ca. 2 mm long and 5 mm wide, puberulous; corolla purplish blue, tubular-campanulate above a narrow neck which is conspicuously curved and enlarged toward the base, 2.5–3 cm long, 1.1–1.3 cm wide at the mouth, the lobes small, less than 5 mm long, the whole tube puberulous outside, glabrous inside except at the stamen insertion; stamens didynamous, the anthers 1-thecate, the second theca reduced to a minute appendage, each theca 3–4 mm long, the staminode 2.5–3 cm long, subexserted, the middle third and apex glandular pubescent; ovary flattened-ovate, 2 mm long, 2 mm wide, densely puberulous. Fruit not seen.

TYPE: ECUADOR. LOJA: Between Panamerican Highway and Zumbi on road to Machala, km. 69, dry quebrada vegetation, 2100 m, 23 Sep. 1967, *Sparre 18862* (MO, holotype).

Additional collection examined: PERU. PIURA: Ayabaca, Oct. 1868, *Raymondi 1252* (USM).

This species is exactly intermediate between *J. acutifolia* H. & B. and *J. mimosifolia* D. Don on the one hand and the *J. caucana* complex on the other. It has the relatively large leaflets and pubescent ovary of *J. caucana* Pittier but the pubescent corolla tube of *J. mimosifolia*. The curvature and enlarged base of the corolla are more pronounced than in *J. acutifolia* but less so than in *J. caucana*. Neither of these species has such reduced corolla lobes nor notably exserted staminodes as

J. sparrei. Jacaranda sparrei is also intermediate geographically: *J. acutifolia* occurs in the dry inter-Andean valleys of Peru, while *J. caucana* occurs from the inter-Andean Cauca and Magdalena valleys of Colombia north to Costa Rica.

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PHYLLARTHRON BILABIATUM: A NEW SPECIES OF BIGNONIACEAE FROM MADAGASCAR

Phyllarthron bilabiatum A. Gentry, sp. nov.—Fig. 1.

A *P. madagascariense* foliis angustis nervatura indistincta, a *P. humblotiano* calyce 5-costato, et ab ambabus foliis verticillatis et calyce bilabiato differt.

Large tree to 25 m tall and 0.7 m d.b.h., the trunk convoluted with deep vertical fissures, the branchlets subterete to subtriangular, glabrous. Leaves verticillate in 3's, of 2 superposed articles; petiole ca. 1 cm long; basal article very narrowly oblanceolate-oblong, cuneate to the base, rounded at the apex, 3.5–7 cm long, 1.5–2.2 cm wide, the second article very narrowly elliptic or elliptic-oblong, rounded at the base, obtuse to subacute or emarginate at the apex, 2–7 cm long, 1–2.6 cm wide; drying olive to gray above, brownish beneath, glabrous, coriaceous, the margins strongly revolute, the secondary nerves very obscure, hardly or not at all visible. Infloresence a short terminal panicle, the lateral branches opposite, each with 1 or 3 flowers; bracts and bracteoles minute, deciduous. Calyx campanulate, strongly bilabiate, 12–13 mm long, 7–9 mm wide, split over ⅓ its length (ca. 5 mm), with 5 conspicuous longitudinal ridges, these terminating in minute denticulations, glandular and drying with a varnished surface, otherwise glabrous. Corolla (single mature corolla seen) magenta with the top of the throat darker, the floor of the throat white with yellow ridges, tubular-infundibuliform, 4.6 cm long, ca. 1.5 cm wide at the mouth of the tube, the tube 2.6 cm long, the lobes 1.2–1.5 cm long, puberulous outside and on the lobes and floor of the tube inside, the lobes also glandular-lepidote. Stamens included, the anther thecae divaricate; pistil and disc not examined. Fruit unknown.

Type: Madagascar. diego-suarez: Tsaratanana Massif, trail up S ridge of Maramokotro, Andohanisambirano, 2,000–2,500 m, montane cloud forest, 9 May 1974, *Gentry 11612* [MO, holotype; P, TAN, Service Forestière (Madagascar), isotypes].

Phyllarthron bilabiatum is most closely related to *P. madagascariense* (Boj.) K. Schum. and *P. humblotianum* Perrier. Its strongly 5-ribbed calyx suggests the former. Its narrow leaves with indistinct venation and revolute margins suggest the latter. Neither of these species has whorled leaves. The leaves of *P. bilabiatum* are conspicuously decurrent so that its branchlets appear almost triangular

FIGURE 1. Habit of *Phyllarthron bilabiatum* A. Gentry (×7/10). [*Gentry 11612* (MO).]

in cross-section. The most noteworthy floral character of this species is a strongly bilabiate calyx which is matched in the genus only by the very different *P. megapterum* Perrier.

Perrier de la Bathie (1938a, 1938b) noted the variability of juvenile leaves of this genus and excluded them from consideration in his key and species descriptions. I have followed suit in using only the mature foliage in the description of the new species. However, a sterile collection from the type locality [*Gentry 11618* (MO) described as a sterile treelet 2 m tall] certainly represents a juvenile form of *P. bilabiatum*. The leaves of this collection are larger and thinner than

mature leaves and have secondary venation approaching that of *P. madagascariense*, but their whorled placement agrees with *P. bilabiatum*. The stem of this plant is distinctively triangular from the strongly decurrent leaves, a character which appears to distinguish juvenile plants of *P. bilabiatum* from juvenile forms of any other species of the genus.

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———. 1938b. Bignoniacées. *In* H. Humbert (editor), Flore de Madagascar, 178e Famille. 91 pp.

—Alwyn H. Gentry, Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

TAXONOMIC NOTES AND NEW COMBINATIONS IN *LEUCOPHYSALIS* (SOLANACEAE)

During the course of a revisionary study of *Chamaesaracha* (Averett, 1973), several species were encountered which, at one time or another, had been assigned to but are clearly not a part of *Chamaesaracha*. Most of these species were relegated, either by me or previous workers, to *Leucophysalis* or the Asian genus *Physaliastrum*. In dealing with the misplaced species, the close relationship of *Physaliastrum* to the North American genus *Leucophysalis* became apparent, but since the species were removed from *Chamaesaracha*, the question of the two being congeneric was postponed (Averett, 1971). The data now at hand indicate that the species of *Physaliastrum* are clearly related to and are best treated as *Leucophysalis*. The latter treatment necessitates several nomenclatural changes. Since my revision of the genus will not appear for several months, it seems advisable to make the following new combinations at this time:

Leucophysalis kweichouense (Kuang & Lu) Averett, comb. nov.

Physaliastrum kweichouense Kuang & Lu, Acta Phytotax. Sin. 10: 351. 1965. TYPE: China, Kweichou Province, Keili, Maopin, 750 m, *Chang Yongtien 1396* (SH, holotype, not seen).

Leucophysalis sinicum (Kuang & Lu) Averett, comb. nov.

Physaliastrum sinicum Kuang & Lu, Acta Phytotax. Sin. 10: 352. 1965. TYPE: China, Shansi Province, *Wei-ying Hsia 4321* (SH, holotype, not seen).

Leucophysalis yunnanense (Kuang & Lu) Averett, comb. nov.

Physaliastrum yunnanense Kuang & Lu, Acta Phytotax. 10: 348. 1965. TYPE: China, Yunnan Province, Sunning, 1800 m, *T. T. Yu 16767* (SH, holotype, not seen).

Leucophysalis japonica (Fr. & Sav.) Averett, comb. nov.

Chamaesarcha japonica Fr. & Sav., Enum. Pl. Jap. 2: 454. 1879. TYPE: Japan, Ito Keiske, Tanaka, *Savatier 2166* (not seen).

C. echinata Yatabe, Bot. Mag. (Tokyo) 5: 355. 1891. TYPE: Not designated.
Physaliastrum echinatum (Yatabe) Makino, Bot. Mag. (Tokyo) 28: 20. 1914.
P. japonicum (Fr. & Sav.) Honda, Bot. Mag. (Tokyo) 45: 139. 1931.
P. japonicum (Fr. & Sav.) Kitamura, Acta Phytotax. Geobot. 6: 19. 1937.

Leucophysalis savatieri (Makino) Averett, comb. nov.

Chamaesarcha savatieri Makino, Illustr. Fl. Jap. I. (11): 1. Oct. 9, 1891. LECTOTYPE: Japan, Kegon, Nikko. Oct. 5, 1890, *Makino s.n.* (MAK).
C. watanabei Yatabe, Bot. Mag. (Tokyo) 5: 315. Oct. 10, 1891.
Physaliastrum savatieri (Makino) Makino, Bot. Mag. (Tokyo) 28: 22. 1914.

Leucophysalis kimurai (Makino) Averett, comb. nov.

Physaliastrum kimurai Makino, J. Jap. Bot. 3: 37. 1926. TYPE: Japan, Musashi Province, Mt. Takao, rare, 24 Oct. 1926, *K. Kimura s.n.* (not seen).
P. savatieri f. *kimurai* (Makino) Ohwi, Fl. Jap. 1026. 1956.

Nine species in total, two North American and seven Asian, are considered to compose the genus *Leucophysalis.*

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———. 1973. Biosystematic study of *Chamaesarcha* (Solanaceae). Rhodora 75: 325–365.

—John E. Averett, Department of Biology, University of Missouri-St. Louis, St. Louis, Missouri 63121.

CHROMOSOME NUMBERS OF PHANEROGAMS. 7[1]

Counts by **Charles Albert Huckins**, Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

ROSACEAE

Malus baccata (L.) Borkhausen. $2n = 34$. U.S.A. WASHINGTON, D.C.: Cultivated, U.S. National Arboretum accession number 2059 (PI 107683), *Huckins 66042101* (BH).

Malus baccata var. *himalaica* (Maximowicz) Schneider. $2n = 34$. U.S.A. MASSACHUSETTS: Cultivated, Arnold Arboretum accession number A101-34-C, *Huckins 69050813* (BH).

Malus florentina (Zuccagni) Schneider. $2n = 34$. U.S.A. WASHINGTON, D.C.: Cultivated, U.S. National Arboretum accession number 3361, *Huckins 67081802* (BH).

Malus fusca (Rafinesque) Schneider. $2n = 34$. U.S.A. NEW YORK: Cultivated, Durand-Eastman Park accession number 77, *Huckins 69052703* (BH).

Malus rockii Rehder. $2n = 51$. U.S.A. MASSACHUSETTS: Cultivated, Arnold Arboretum accession number A 83-84, *Huckins 70051902* (BH).

[1] The previous number in this series appeared in Ann. Missouri Bot. Gard. 62: 513. 1975.

Malus sikkimensis (Wenzig) Koehne ex Schneider. $2n = 51$. U.S.A. NEW YORK: Cultivated, Durand-Eastman Park accession number 841, *Huckins 69052105* (BH).

Malus tschonoskii (Maximowicz) Schneider. $2n = 34$. U.S.A. NEW YORK: Cultivated, Cornell University Horticulture Department accession number URI-12, *Huckins 68041701* (BH).

Malus yunnanensis (Franchet) Schneider. $2n = 34$. U.S.A. NEW YORK: Cultivated, Cornell University Horticulture Department accession number URI-4, *Huckins 69050601* (BH).

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 63, No. 4, pp. 657–896, was published on 14 June 1977.

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CHEMOSYSTEMATICS: THE TWENTY-THIRD SYSTEMATICS SYMPOSIUM

JOHN E. AVERETT[1]

The following seven papers were presented at the Missouri Botanical Garden's Twenty-third Annual Systematics Symposium held 15–16 October 1976. The symposium, sponsored in part by the National Science Foundation, was attended by approximately 300 scientists. This year's topic was chemosystematics.

The studies of R. E. Alston and B. L. Turner in the early 1960s which utilized flavonoid patterns in elucidating complex hybridization and their publication of *Biochemical Systematics* in 1963 were instrumental in bringing chemistry to the systematic community. In 1962 the first international conference on biochemical systematics was held, and the proceedings were published the following year in *Chemical Plant Taxonomy* (Swain, 1963). *Taxonomic Biochemistry and Serology*, also proceedings of an international conference held in 1962, appeared in 1964 (Leone, 1964). Through the 1960s numerous papers dealing with natural products appeared in the literature and by 1970 the field of biochemical systematics or chemotaxonomy was well established.

In 1972 the International Union of Pure and Applied Chemistry held a symposium in Strasbourg on "Chemistry in Evolution and Systematics" (Swain, 1973). In the following year the topic of the 25th Nobel Symposium was "Chemistry in Botanical Classification" (Bendz & Santesson, 1974). The latter was an attempt to bring chemists and taxonomists together, in what V. H. Heywood has referred to as the unlikely marriage of an exact science with one less restricted that ventures into every other discipline.

Early studies utilized compounds, and except for serology, largely secondary compounds, in resolving hybridization complexes or as "finger prints" for characterizing species or, occasionally, higher taxa. However, concomitant with the development of the field, techniques and instrumentation necessary for the isolation and structural characterization of the compounds were refined. Further,

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information on biosynthetic pathways and genetics of the secondary compounds accumulated. Now it is relatively easy to assay the complex constitution of a plant. Structural and biosynthetic data greatly enhance the utility of the compounds in phylogenetic interpretations. The extent to which this is true, as well as the sophistication that has developed within the field, is well illustrated in the following papers.

Following the format of the symposium, the first three papers discuss the utility of macromolecules and next three papers discuss micromolecules. The final paper on the effect of chemistry upon traditional taxonomists was presented as an evening talk by B. L. Turner.

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PERSPECTIVES IN PLANT SEROTAXONOMY[1]

DAVID E. FAIRBROTHERS[2]

ABSTRACT

The capacity to view recent data in proper relation to other information, or the ability to correctly judge the significance of facts and ideas, requires a knowledge of both the past mistakes and the forward strides within a discipline. This paper is intended to help the reader formulate perspectives concerning 65 years of plant serotaxonomic research. The discovery that the immune reaction was only relatively specific and that the degree of cross-reactivity was essentially proportional to the degree of relationships between organisms had important implications for comparative systematic serology. It is the specific reactions, between determinants and antideterminants, which provide a measurement of protein similarities. The comparison of protein mixtures, rather than purified single proteins, has dominated taxonomic research because such an approach provides serological overall similarity, and thus a multicharacter comparison. The "antisystematic" reactions have recently been shown to result from variation in the systematic ranges of determinants; and the absorption (presaturation) technique for removing common determinants increases the accuracy of serological placements. The following items were evaluated: antigenic preparations, adjuvants, injection procedures, single versus mixed protein extractions, kind of plant tissue extracted, and the interference of secondary compounds. *Cornus canadensis* and *C. suecica* were found to be serologically very similar. The tested species of the genus *Cornus* were divided into three distinct serological groupings. The serological data support the separation of the Cornaceae and Nyssaceae; and the inclusion of *Camptotheca* and *Nyssa* in the Nyssoideae, and *Davidia* in the Davidioideae, both of the family *Nyssaceae*. *Nyssa biflora* and *N. sylvatica* were serologically very similar; *N. ogeche* and *N. aquatica* were serologically distinct from each other and from *N. biflora* and *N. sylvatica*. *Nyssa ogeche* was the most distinct species of the genus. *Corokia cotoneaster* had very little serological similarity with any of the tested species of the Cornales.

To have the capacity to view recent data in proper relation to other information, or the ability to correctly judge the significance of facts and ideas, requires a knowledge of past mistakes and the forward strides within a discipline. It also requires a degree of knowledge of the individual components as well as the total products resulting from the various component combinations. The author hopes this manuscript will provide the reader with the necessary information and literature citations which will allow the formulation of perspectives concerning 65 years of plant serotaxonomic research.

The "present age" of chemosystematics or chemotaxonomic publications commenced to appear in the early 1950's. The oldest of the "present age" approaches is serotaxonomy and the newest is amino acid sequencing (Cronquist, 1976).

The discovery of serological reactions in Austria via the occurrence of precipitin reactions took place 80 years ago (Kraus, 1897). This discovery provided a new technique which was soon used to aid in the investigation of systematic problems in animals. Within two years after the discovery of the precipitin re-

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[1] I dedicate this publication to the memory of my friend and fellow phytoserologist, Dr. Josef Kloz, who died in his 55th year on October 22, 1976 in Czechoslovakia.

The research was supported by NSF Grants GB-13202 and BMS 75-17805.

[2] Department of Botany, Rutgers University, New Brunswick, New Jersey 08903.

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action the technique was applied to comparative problems by the Frenchman Bordet (1899). This was followed by a series of extensive comparative studies which were conducted with various animals by the Englishman Nuttall (1901, 1904). Thus biologists have known for 75 years that organisms may share antigenic material (substances capable of inducing the formation of antibodies and able to react with the antibodies); and that when they share the same antigenic material in different proportions it is assumed that the organisms are related. At first it was believed that the immune reaction was absolutely specific, that is, that an antiserum would react only with the antigen that stimulated its production. However, Bordet (1899) in conducting research with birds reported that the reaction was only relatively specific and that the degree of cross-reactivity was essentially proportional to the degree of relationships between organisms. It was this early discovery which had important implications for systematics and started the pioneer investigations in the discipline of comparative animal systematic serology.

A large number of animal systematic serological publications have been reported in the bibliography prepared by Leone (1968) and the book edited by Wright (1974). The pioneering work in the United States essentially began with Boyden (1926), and he has continuously contributed to the field of animal systematic serology for 50 years (Boyden, 1973; Wright, 1974). Approximately 550 plant taxa (cultivars through orders) have been included in approximately 160 systematic serological publications since 1950 (Fairbrothers, 1969a; Fairbrothers et al., 1975).

Serology is concerned with the interactions of antigens and antibodies and/or antibodylike substances, the lectins. The term "serology" is often used synonymously with immunology. However, some biologists prefer "serology" because "immunology" has an implication that immunity is concerned in all reactions between antigens and antibodies (Boyden, 1948).

Principles of Serology

A consideration of a few basic facts related to the biology of the immune response is a valuable aid to understanding the methods and interpretations of systematic serological research.

The term "antigenic" is relative since the response is frequently a property of the route of injection, method of preparation of the antigenic material, and the individual experimental animal used. Thus it is important that details about such items and procedures should always be included as a portion of the methods and materials section of publications. Experimental data have demonstrated the following: (1) There is a certain minimal molecular weight below which substances are not in themselves antigenic. Some of the lower molecular weight substances can become antigenic by mixing them with other substances (adjuvants). (2) Size alone is not enough to guarantee that a molecule will be antigenic. Immunochemists indicate that the specific action is in part due to the rigidity of certain chemical structures (determinants) which are difficult to distort or alter. (3) Usually a molecule must be foreign to an organism to be immunogenic. (4) Substances must be soluble or be able to be broken down

into soluble antigenic components before being capable of inducing antibody formation. (5) Too much antigenic material may cause immunological paralysis (i.e., cannot be immunized). There appears to be a balance between stimulation and paralysis for each antigenic material. (6) Many proteins have been found to be immunogenic, and the best known immunogens are the proteins with molecular weights of 40,000 or more (Abramoff & La Via, 1970).

Of the several kinds of serological reactions, the precipitin reaction has been used most frequently in plant comparative serological investigations. It is a relatively simple reaction capable of being applied to the comparison of the soluble protein antigenic material extracted from all kinds of plants. Microcomplement fixation has proved valuable in animal systematics (Champion, et al., 1974), but has had practically no application in comparable plant research. Serological research can be conducted employing quantitative precipitation, precipitin techniques in solutions, or by various qualitative precipitation techniques in gels. The serological characteristics of proteins are linked with the primary structure of the molecule. The reaction is concerned with points on the molecule (determinants) which are capable of initiating the production of immuno-globulins only in certain cells of animals (not plants). These immuno-globulins possess properties accounting for the bonding to the respective protein reaction position. Thus the serological characteristics of the protein are found in the determinants, which are restricted to certain positions of the molecules.

A fairly accurate estimation of the size of determinants has been obtained from protein fractionation experiments designed to detect the smallest molecule fraction still capable of an immunological response. Arnon & Sela (1969) and others have demonstrated that the active antigenic regions of proteins are composed of 10–20 amino acids.

Systematists and taxonomists are interested in the comparison of antigenic determinants from various taxa. It is the specific reactions between determinants (antigens) and antideterminants (antibodies) which are valuable because they provide a means for the measurement of protein similarities.

Methodology

When deciding the type of antigenic preparation, the process of denaturation, which means structural changes with concomitant loss of biological properties, must be taken into account. Protein antigens are not equal in susceptibility to denaturation. However, all such changes result in some loss of original specificity.

The use or nonuse of adjuvants (Freund's, in our experiments) to increase the level of an immune response (immuno-enhancement) is discussed in systematic serological research. The purpose of an adjuvant is to heighten and prolong the immune response; and the value of this additional material must be judged for each antigenic material. This means its use or nonuse should be decided after experimentation.

The effect of injection procedures on the systematic reaction range has been tested by various experiments. One of the very early reports indicating that longer immunization periods extend the reaction range was conducted with a *Zea mays*

antiserum (Magnus, 1908). Lake et al. (1914) using purified seed protein material in contrast to crude seed extracts as used by Magnus also found that a longer injection period extended the reaction range of the antisera. Several recent publications, with both plant and animal antigens in the form of purified or mixed reagents, indicate that the systematic reaction ranges of antisera are extended by injections continued until a maximum reaction is reached (Boyden, 1971, 1973). Such experiments indicate also that long continued immunization is likely to induce the formation of greater proportions of cross-reacting antibodies, which will reduce the discriminating capacity of the antiserum. Antisera derived from several and long injection periods may reach a higher level of "fidelity" to mixed antigens, and reveal information of value in systematic research (Moritz, 1964). Leone (1952) demonstrated that longer immunization periods tend to cause a lower discriminating capacity.

Therefore, the number of injection series used should be stated so the reader can make proper comparisons. The use of a combination of "short" and "long" injection series may produce the largest amount of data for comparative serological investigations. This should not be considered experimental "manipulation" because it is merely using serological techniques to the fullest advantage based upon our present knowledge of the immune response.

There are two main approaches to serological research: (1) comparison of single proteins, or (2) comparison of protein mixtures. The second approach has dominated taxonomic research (Moritz, 1964; Fairbrothers, 1968; Jensen, 1974a). An example of the comparison of a single protein is best illustrated by the research with phaseolin obtained from *Phaseolus vulgaris*, and the ribulose-1,5 biphosphate carboxylase ("fraction I") found in green plants. Data obtained from such research indicates that the systematic ranges of determinants vary. Some determinants are found throughout the plant kingdom, while others have a very restricted distribution. In general, the low taxonomic yield from single protein investigations has not justified the large preparation effort required (Jensen, 1974a). Serological comparison of protein mixtures which were extracted from seeds, pollen, spores, tubers, or leaves is most common. The results provide a serological overall similarity and thus a multicharacter comparison. Researchers working with plant protein extracts also find tannins, saponins, alkaloids, lipids, and/or polysaccharides, which may have to be inactivated, reduced, or eliminated by diverse extraction procedures.

When using a pure protein, only a very limited number of determinants can be compared. In contrast, when using mixtures of proteins, data from many different determinants are tested, and thus the chances of being misled in terms of serological correspondence are lessened.

"Antisystematic" Reactions

A phenomenon which has been designated "antisystematic," "asystematic," or "unexpected" cross-reactions has only very recently been placed in proper perspective (Moritz & Rohn, 1956; Frohne et al., 1961; Moritz, 1964). Jensen (1974a, 1974b) indicated that these terms are no longer used by the above authors because past usage assumed serological convergence, which has been shown not to

be the causative agent for such responses. Moritz (1964) included several reports which illustrated his designated "antisystematic" reaction. He also indicated why such reactions were specific serological reactions, and not some kind of non-specific effect, since they disappeared when presaturation experiments were conducted.

The practice of some researchers during the last several years of designating cross-reactions with a wide systematic range as "antisystematic" should be discontinued. Such wide-range reactions are the result of certain determinants being widely distributed in the plant kingdom. In other words, they should be considered as reactions of determinants that are widespread and remain relatively constant. One such determinant has been demonstrated by the serological research with Fraction I Protein (ribulose-1,5 biphosphate carboxylase) extracted from the tissue of green plants. The serological partial identity detected between wide-ranging taxonomic groups has been shown to be the result of parts of the protein structure unaltered in the course of long periods of evolution (Sugiyama et al., 1969; Jensen, 1974a, 1974b). Thus we now know that the systematic ranges of determinants do vary, and sometimes protein molecules carry several determinants which reveal partial serological identities.

The understanding of the above reactions is important because it has shown the value of the presaturation (absorption) technique for removing common determinants and leaving only those systems specific for each taxon compared, thus providing both a more accurate serological placement and measure of the relative similarity.

The use of various techniques to remove nonspecific reactants which react with normal rabbit serum (NRS) has become standard practice in present-day plant serological research. We now know such responses often come from serological reactions resulting from the presence of lectins. Lectins can be removed by hemagglutination techniques and thus be prevented from interfering with normal serological reactions (Lee & Fairbrothers, 1972).

Thus in recent years experiments have provided answers to some of the former perplexing problems associated with plant systematic serological research. This has been very valuable and allowed the continued development of such research. It also assures that a larger spectrum of species can be compared by using the techniques which are now available, and our percentage of accuracy in terms of serological placements, is continuing to increase.

History of Plant Serology

As with animals, serological techniques were used in plant systematics and taxonomy soon after discovery. Mez of the Botanical Institute, University of Königsberg, Germany, conducted such research with his students and colleagues from 1911–1936 (Mez & Gohlke, 1914; Mez, 1922). The "Königsberger Serodiagnostik Stammbaum" (phylogenetic tree) was the climax of years of research (Mez & Ziegenspeck, 1926). This group was known as the Königsberg Serological School, in contrast to the Berlin Serological School which was headed by Professors Gilg and Schürhoff, who conducted research during the 1920's (Gilg & Schürhoff, 1926). These two groups of researchers (schools) conducted a

literary feud which seriously jeopardized the credibility of plant systematic serological research for essentially 25 years. The techniques employed in the early research proved to have several serious flaws. Mez's technique, where he produced an immune serum through the influence of antigen on serum and eliminated the use of living animals as antisera producers, was a serological "disaster." The vast amount of data reported using this procedure was not valid and has been disregarded.

It was Moritz (1928, 1964) and his colleagues at the University of Kiel, Germany, who, working from 1928 until the present, revealed the value of serological research for plant systematics. Jensen, formerly from Kiel, has recently organized another serological laboratory at the University of Cologne. Frohne continues the systematic serological research at Kiel.

In the United States Chester published plant serological papers in the 1920's and 1930's and also prepared a comprehensive critique about plant systematic serology (Chester, 1937). In 1947 Johnson (1951), with his students, started the present United States trend toward plant systematic serological research. It was he who introduced me to the techniques in 1957 after I had joined the faculty of Rutgers University.

In 1953 Urano (1955) started phytoserological investigations in Japan, and S. Sakaguchi and S. Arai have continued this research (Fairbrothers, 1969a). The *Solanum* serological research in Birmingham, England was started in 1955 (Gell et al., 1956). J. Hawkes (Birmingham) and his students (Lester and P. M. Smith) have continued serological research to the present time. In Prague, Czechoslovakia in the late 1950's the husband and wife team, Kloz and Klozova, started and continued serological investigations of *Vicia faba* and other legumes (Kloz et al., 1960). The year 1963 saw the start of another plant serological research center headed by Vaughan in London, and he has continued his multidisciplinary *Brassica* investigations to the present time (Vaughan & Waite, 1965; Vaughan et al., 1976). Cristofolini (1968) has published several reports from his botanical laboratory in Italy since beginning his plant serological research in 1966. The most recently organized plant systematic serological laboratory is under the leadership of Drs. Morozova, Chupov and Kutjavina at the Komarov Botanical Institute, Leningrad, USSR (Fairbrothers, 1975).

Interpreting the Results

Research has demonstrated that extracts of seeds, pollen, leaves, tubers, and spores of vascular plants can be used, if the required extraction procedures are followed (Fairbrothers, 1969b, 1975; Fairbrothers et al., 1975). However, most systematic serological research has included seed material, due to the relatively high concentration of proteins, relative ease of collecting, and relative ease of assuring comparable developmental stages. We are presently pursuing the following two new studies in our chemosystematic laboratory using pollen as the source of protein material: (1) serological investigation of selected amentiferous taxa with Frank Petersen, and (2) a serological investigation of the Corylaceae (Betulaceae) with Friedrich Brunner.

Phytoserological research has provided provocative and valuable data for use in the classification of flowering plants. The numerous examples cited in the evaluation of the contribution of serological data related to Cronquist's and Takhtajan's systems of classification were shown to be significant (Fairbrothers et al., 1975). This publication indicates that such data have contributed in the classification of the following orders, and the placement of families within these orders: Capparales, Caryophyllales, Cornales, Dipsacales, Illiciales, Lamiales, Magnoliales, Nelumbonales, Nymphaeales, Papaverales, Polemoniales, Ranunculales, Rubiales, Scrophulariales, Typhales, and Umbellales. In addition to these orders, significant contributions have also been published for species, genera, and/or tribes belonging to the following families: Ammiaceae, Berberidaceae, Brassicaceae, Caprifoliaceae, Cucurbitaceae, Chenopodiaceae, Cornaceae, Fabaceae, Lamiaceae, Magnoliaceae, Nelumbonaceae, Nymphaeaceae, Nyssaceae, Papaveraceae, Poaceae, Ranunculaceae, Solanaceae, and Typhaceae.

The serologic and disc electrophoretic characterization and comparison of the spore proteins extracted from *Osmunda cinnamomea*, *O. claytoniana*, and *O. regalis* illustrated that fern spores were suitable material for such analyses. *Osmunda cinnamomea* and *O. claytoniana* were shown to possess greater protein affinities for each other than either had for *O. regalis*. *Osmunda regalis*, in general, had greater protein affinities for *O. claytoniana* than it had for *O. cinnamomea* (Petersen & Fairbrothers, 1971). Stein & Thompson (1975) compared the same three *Osmunda* species using DNA hybridization techniques and independently indicated the same relationships reported by Petersen & Fairbrothers (1971). Miller (1967), based on anatomical characters of living and fossil specimens, indicated that *O. claytoniana* and *O. regalis* were more closely related, while Hewitson's (1963) anatomical and morphological research indicated that *O. cinnamomea* and *O. claytoniana* had a closer relationship with each other than either had with *O. regalis*.

The serological investigation of intra- and interfamily relationships of the Cornaceae and Nyssaceae has continued intermittently in our chemosystematics laboratory for 15 years, and various experiments have been conducted as appropriate and adequate plant materials became available. In our systematic serological research it has been expedient to conduct several projects simultaneously because no experiments can be conducted until adequate and appropriate materials are available for the extraction of proteins, and until antisera to perform the essential experiments have been raised.

Cornus canadensis and *C. suecica* have been found serologically very similar based on photronreflectometer tests, Ouchterlony plates, and absorped and nonabsorbed antisera. These two taxa have also been shown to be the most dissimilar from other taxa placed in the genus *Cornus* (Fairbrothers, 1966a, 1966b, 1968). When data were evaluated from cytology, morphology, anatomy, geographical distribution, and the putative hybrid (*C. unalaschkensis*), the close similarity between the two was also detected. I believe all the data indicate that the two named taxa are subspecies of one circumboreal species which is very distinct from the other species of *Cornus*. If there is justification for dividing the genus *Cornus* into distinct genera, then this species (or two species) would

TABLE 1.[a] Data obtained from precipitin reactions with species of *Camptotheca* (Ca.), *Cornus* (C.), *Corokia* (Co.), *Davidia* (D.), and *Nyssa* (N.) using the photronreflectometer. The numbers represent percent area of the reference reaction, which is expressed as 100%.

Antigens	Antisera[b]										
	C. amomum R-110^{5}	*C. amomum* R-118^{4}	*C. canadensis* R-106^{5}	*C. racemosa* R-124^{4}	*C. racemosa* R-125^{5}	*N. aquatica* R-98^{4}	*N. aquatica* R-111^{3}	*N. ogeche* R-112^{4}	*N. sylvatica* R-114^{4}	*N. sylvatica* R-116^{5}	*D. involucrata* R-105^{4}
C. amomum	100	100	50	90	84	56	32	32	27	47	—
C. stolonifera	81	—	—	—	—	—	—	—	—	—	—
C. racemosa	73	84	49	100	100	57	33	28	26	45	—
C. florida	54	—	—	—	65	—	—	—	—	—	—
C. kousa	48	—	—	—	60	—	—	—	—	—	—
C. nuttallii	50	—	—	—	62	—	—	—	—	—	—
C. canadensis	—	38	100	—	46	35	—	15	—	28	—
Ca. acuminata	30	33	25	34	38	69	50	47	44	65	39
N. aquatica	36	26	15	—	30	100	100	76	66	92	—
N. ogeche	—	26	12	—	20	89	—	100	—	86	—
N. sylvatica	33	31	15	34	20	94	83	83	100	100	52
D. involucrata	23	—	—	31	—	—	41	—	34	—	100
Co. cotoneaster	7	—	—	3	10	—	10	10	4	—	5

[a] It is essential that these new data be evaluated with previous published photronreflectometer data for some of the included taxa (Fairbrothers & Johnson, 1964; Fairbrothers, 1966a, 1966b, 1968).

[b] The superscripts on the antisera numbers indicate the number of injection series each experimental animal received.

TABLE 2.[a] Number of immunoprecipitating systems (bands) obtained from Ouchterlony Plates (double diffusion) for *Cornus* (C.), *Camptotheca* (Ca.), *Corokia* (Co.), *Davidia* (D.), and *Nyssa* (N.). Seven antisera are compared with nine antigens.

	Antisera[b]																				
	C. amomum R-110^{5}			*C. canadensis* R-106^{5}			*C. racemosa* R-124^{4}			*N. aquatica* R-98^{4}			*N. ogeche* R-112^{4}			*N. sylvatica* R-116^{5}			*D. involucrata* R-105^{4}		
	Banding Patterns[c]																				
Antigens	I	N	T	I	N	T	I	N	T	I	N	T	I	N	T	I	N	T	I	N	T
C. amomum	5	0	5	1	1	2	2	1	3	1	1	2	0	2	2	1	1	2	1	1	2
C. racemosa	2	1	3	1	1	2	4	0	4	1	1	2	0	2	2	1	1	2	1	1	2
C. canadensis	0	2	2	4	0	4	1	1	2	0	2	2	0	1	1	0	2	2	0	2	2
Ca. acuminata	1	1	2	0	1	1	1	1	2	1	2	3	1	1	2	2	1	3	2	1	3
N. aquatica	1	1	2	0	1	1	0	2	2	4	0	4	3	0	3	3	0	3	2	1	3
N. ogeche	1	1	2	0	1	1	0	2	2	2	1	3	4	0	4	2	1	3	—	—	—
N. sylvatica	1	1	2	0	1	1	0	1	1	3	1	4	2	1	3	5	0	5	2	1	3
D. involucrata	—	—	—	—	—	—	1	1	2	—	—	—	—	—	—	1	2	3	4	0	4
Co. cotoneaster	0	1	1	0	1	1	0	1	1	0	2	2	0	1	1	0	1	1	0	2	2

[a] It is essential that these new data be evaluated with previous published serological data for some of the included taxa (Fairbrothers & Johnson, 1964; Fairbrothers, 1966a, 1966b, 1968).

[b] The superscripts on the antisera numbers indicate the number of injection series each experimental animal received.

[c] Banding patterns have been designated as follows: I = identity bands, N = nonidentity and/or partial identity bands, T = total number of bands.

best qualify for such a designation, and would have to be given the generic name of *Chamaepericlymenum.*

Serological data have also indicated that within the genus *Cornus* there are the following three distinct groupings: (1) *C. florida, C. kousa,* and *C. nuttallii;* (2) *C. amomum, C. stolonifera,* and *C. racemosa;* and (3) *C. canadensis* and *C. suecica* (Fairbrothers & Johnson, 1964; Fairbrothers, 1966a, 1966b, 1968). These serological groupings correspond to the *Cornus* subgenera designated by Ferguson (1966), except he placed *C. kousa* in a subgenus distinct from that containing *C. florida* and *C. nuttallii.* Newer serological data from our laboratory based upon additional antisera and many more experiments continue to support a tripartite taxonomic disposition of the taxa placed in the genus *Cornus* (Tables 1–2). The use of nonflavonoid glucosides as taxonomic markers in the genus *Cornus* was reported by Jensen et al. (1975). Their suggested arrangement of subgenera based on the presence or absence of iridoids, plus the type of iridoid constituents agree with the reported serological groupings and would correspond to their (A/B), (C), and (F/G/H) designations.

The families Cornaceae and Nyssaceae were recognized by Dumortier in 1829. However, this separation into two families was not followed by most taxonomists for over 100 years. Recently Melchior (1964), Cronquist (1968), Thorne (1968, 1976), Takhtajan (1969), and Dahlgren (1975) have recognized two families. In addition, in most recent classifications the genus *Davidia* has been removed from the Nyssaceae and placed in the Davidiaceae (Melchior, 1964; Cronquist, 1968; Takhtajan, 1969; Dahlgren, 1975). Thorne (1968, 1976) placed *Davidia* in the subfamily Davidioideae of Nyssaceae following Wagerin (1910). Harms (1898) was the first author to use the two subfamilies Davidioideae and Nyssoideae, and he placed them both in the family Cornaceae.

The serological data support the separation of the Cornaceae and Nyssaceae, and the grouping of *Camptotheca, Davidia,* and *Nyssa* within the Nyssaceae (Tables 1–2). At present I believe the serological data best support the placement of *Davidia* in the Davidioideae, and *Camptotheca* and *Nyssa* in the Nyssoideae both of the family Nyssaceae (Fairbrothers & Johnson, 1964; Fairbrothers, 1966a, 1966b, 1968; Tables 1–2).

Perdue et al. (1970) reported that tests with *Camptotheca acuminata* demonstrated that crude extracts exhibited significant activity against lymphoid leukemia. This comprehensive report discussed the relationships of *Camptotheca* within the Nyssaceae, indicating that *Camptotheca* was closely related to *Nyssa* and only remotely related to *Davidia.* Research done by Titman (1949) using wood anatomy, Eyde (1963) using fruit structure and the fossil record, and Sohma (1963) using pollen support the taxonomic conclusions of Perdue et al. (1970). Our recent serological data also indicate that *Camptotheca* is more similar to *Nyssa* than to *Davidia,* and that *Nyssa* is more similar to *Davidia* than is *Camptotheca* (Tables 1–2).

Our serological data are also supported in part by the findings of Hohn & Meinschein (1976) based on the fatty acid composition of seeds. They indicated that primitive *Davidia* and advanced *Camptotheca* were placed on each side of *Nyssa,* which is intermediate. Thus all the data presented lend credence

to the placement of *Camptotheca* and *Nyssa* in the subfamily Nyssoideae and *Davidia* in the Davidioideae of the Nyssaceae.

Serological experiments with four species of *Nyssa* have included comparisons of *Nyssa aquatica*, *N. biflora*, *N. ogeche*, and *N. sylvatica*. The various experiments indicated that *N. biflora* and *N. sylvatica* were serologically very similar. *Nyssa ogeche* and *N. aquatica* were serologically distinct from each other and from *N. biflora* and *N. sylvatica*. The data also showed that serologically *N. aquatica* was more similar to *N. biflora* and *N. sylvatica* than to *N. ogeche*. However, *N. ogeche* was more similar to *N. aquatica* than to *N. biflora* and *N. sylvatica*. *Nyssa ogeche* was the most distinct species of the four compared (Fairbrothers & Johnson, 1964; Fairbrothers, 1966a, 1966b, 1968; Tables 1–2). The serological data support the conclusions of both Eyde (1963) and Sohma (1963), who reported close similarity between *N. biflora* and *N. sylvatica* and treated them as two varieties of one species. The serological data does not support the findings of Hohn & Meinschein (1976) based on seed oil fatty acids. They indicated *N. biflora* and *N. sylvatica* to be chemically distinguishable species. The various researchers agree that *N. ogeche* is the most distinct from the other three species of *Nyssa*. The serological data has not clearly indicated whether *Camptotheca*, *Davidia*, or *Nyssa* has the greatest similarity with *Cornus*. The three genera are serologically relatively similar to *Cornus*; however, the data indicate that *Camptotheca* might have slightly more similarity with *Cornus* than do *Nyssa* or *Davidia* (Tables 1–2).

The genus *Corokia* (6 species) is restricted to the South Pacific region, ranging from northern New South Wales, Lord Howe Island, New Zealand, Chatham Islands, and Rapa Island, a distance of 4,000 miles.

The serological data reveal very little similarity between *Corokia cotoneaster* and any species of the Cornaceae and Nyssaceae tested (Fairbrothers et al., 1975; Tables 1–2).

Most researchers have indicated that this genus has little affinity with members of the Cornaceae in which it is often placed. Some botanists have suggested an affinity with the Saxifragaceae within the subfamily Escallonioideae (Escalloniaceae) (Philipson, 1967; Smith, 1958). Eyde (1966, 1967) concluded that it was unrelated to *Cornus* but was possibly linked with *Argophyllum*. Kubitski (1963) retained the genus in the Cornaceae. Hegnauer (1965) indicated that the Cornaceae may be related to either the Saxifragaceae or Loganiaceae. Takhtajan (1969) excluded the genus *Corokia* from the Cornales and placed it in the Escalloniaceae (Saxifragales). Cronquist (1968) considered *Corokia* as a possible nonmissing link between the Cornaceae and Escalloniaceae, Grossulariaceae, or Saxifragaceae sensu lato. Both Cronquist's and Takhtajan's classifications reflect the serological data which indicate the distinctiveness of *Corokia* from members of the *Cornales*.

However, Bate-Smith et al. (1975) investigated the distribution of several chemical compounds in the Cornales and concluded that *Corokia* possesses a chemical pattern consistent with that of the Cornaceae.

The experimental investigation of taxa within the Cornales has indicated that the use of diverse disciplines has provided valuable data for helping to

understand the evolutionary development and relationships of the families and genera in the order. This order has proven to have been an excellent one for diverse chemosystematic research. Serological comparisons have provided significant data for evaluation in the continuing investigation of diverse cornaceous, sensu lato, taxa.

Taxonomy eventually must strive to bring together, summarize, and utilize what is known about the organisms to be compared. Systematic serologists have essentially learned to use the properties of one of the classes of proteins, gamma globulins, in comparative studies. Systematic serology provides comparisons which are relatively objective measurements; however, like all detected relationships, they are relative and not absolute. Thus, as stated in the first paragraph of this paper, I hope that the included information has helped the reader to formulate perspectives concerning plant serotaxonomic research.

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ELECTROPHORETIC EVIDENCE AND PLANT SYSTEMATICS

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Abstract

The study of phenotypes and their variation often provides evidence for phylogenetic inferences in plant systematics. Therefore, it is critical that the phenotypes analyzed reflect as directly as possible the underlying genotypes. The equation between phenotype and genotype is simpler and better understood for evidence obtained by electrophoresis of plant enzymes than for most morphological characters. This article discusses the advantages and limitations of electrophoretic evidence to test hypotheses in plant systematics and evolution. It also summarizes the results of a large number of studies which have utilized this evidence. Three general observations from these studies are: (1). Conspecific plant populations are extremely similar genetically as documented by their very high mean genetic identities, 0.95 ± 0.02. This result suggests that one or a few populations often constitute an adequate sample of a species. (2). Congeneric plant species have strikingly reduced mean genetic identities, 0.67 $\pm$ 0.07. However, certain pairs of annual plant species have genetic identities similar to those of conspecific populations. In these cases, the species have been shown to be related as progenitor and derivative with the derivative being of recent origin. (3). The amount of genetic variability within plant populations appears closely correlated with their breeding system, with outcrossing populations substantially more variable than inbreeding ones. The article also describes a number of actual and potential applications of electrophoresis in plant systematics.

Evidence obtained by electrophoresis of enzymes has not been widely utilized by plant systematists although it has dominated the research of many of their zoological counterparts and population geneticists (Manwell & Baker, 1970; Lewontin, 1974; Nei, 1975; Ayala, 1976). This has meant that the strengths and weaknesses of such evidence for solving systematic and evolutionary questions in plant biology have not been sufficiently discussed. The present article is designed to facilitate an efficient evaluation, and emphasizes the unique characteristics of electrophoretic evidence, the requirements for its analysis, and actual and potential applications in plant systematics and evolution.

Electrophoretic Evidence: Advantages and Limitations

The systematist analyzes phenotypes and their variation and often uses this evidence for phylogenetic inference. Such inferences require that observed phenotypes have a specifiable relationship to unobserved genotypes. The equation between phenotype and genotype is simpler and better understood for electrophoretic evidence than it is for evidence obtained from morphological characters or chromatographic comparisons of secondary metabolites. This follows from the colinearity of amino acid sequence and nucleotide sequence as well as the specificity of enzyme catalysis. It also reflects the fact that electrophoretic evidence is used to answer a very different kind of question than has usually been posed by systematists.

Morphological analysis answers a question such as: Are flower petals with

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conspicuously lobed limbs present in taxon *A* and taxon *B*? Chromatographic analysis asks, for example: Is apigenin present in both taxon *A* and taxon *B*? In contrast, electrophoresis answers a question of a different kind: Does glutamate dehydrogenase have the same electrophoretic mobility(ies) in taxon *A* and taxon *B*? Such a question probes the physical properties of particular enzymes or other proteins on the hypothesis that these properties reveal, to a large degree, the record of accumulated mutations that have taken place in the gene specifying the enzyme. And that when a number of enzymes are considered simultaneously, this record can be evaluated with more precision and objectivity than highly complex morphological features.

The primary observed evidence in studies of electrophoretic variation in natural populations is bands of color in a slab of starch or acrylamide gel. These mark the positions reached by different molecular forms of an enzyme (or other protein) which have migrated through the gel under the influence of an electric field. The enzyme variants are separated because they have different electrostatic charges (a function of the relative number of amino acids with positive and negative charges on their surface). Their migration through the gel may also be differentially affected by their size or configuration. Following their physical separation, the enzymes are identified by a staining reaction based on their catalytic activities. The combination of electrophoresis and staining specificity makes it possible to distinguish particular enzymes among hundreds that may be present in a crude tissue extract.

The different molecular forms of an enzyme that catalyze the same reaction are called isozymes if their polypeptide constituents are coded by more than one gene locus (e.g., lactate dehydrogenase, human ADH). They are called allozymes if their polypeptides are specified by different alleles at a single gene locus; the majority of enzymes routinely studied in natural populations have different allozymic forms.

Allozymes are the biochemical consequence of the substitution, deletion, or addition of amino acids in the polypeptides which comprise the enzyme, and they can be distinguished if these changes affect their electrophoretic migration. Since the amino acid sequence of a polypeptide is colinear to the nucleotide sequence of its coding structural gene locus, allozymes result from gene mutation. Thus, an analysis of protein structure using electrophoresis is, to a first approximation, an analysis of a gene. It is precisely this simple relationship between the bands of color on the gel and the nucleotide sequence of genes that makes protein electrophoresis a powerful analytic tool for systematics.

A major advantage of electrophoretic evidence is that colinearity assures that systematic comparisons can be made between products of genes which are homologous (have a common origin), thus, avoiding problems of convergence and functional correlation often prevalent with morphological characters. Another important advantage is that electrophoretic evidence is precise and directly quantifiable in terms of the number and kinds of enzymes studied, permitting the amount of genetic information utilized to be stated exactly. This is seldom possible with morphological or other characters. A third significant advantage is that comparisons are made with enzymes that are generally always

present (with the exception of those selectively turned on or off during development) and little influenced by environmental factors. This avoids the frequent situation that occurs with both morphological and chromatographic data in which the absence of a character in one taxon is interpreted as an indication of a less close phylogenetic relationship between it and other taxa that display the character even though independent evidence is lacking regarding the cause of the character's absence. Another advantage is that problems of a priori character weighting do not occur with electrophoretic evidence because all enzymes examined are accorded equal value in similarity matrices or other methods of evaluating divergence.

The theoretical advantages of electrophoretic evidence, to be sure, are offset by certain shortcomings but, fortunately, these are reasonably well defined. The first problem is that a small number of enzymes is sampled and these may not represent enzymes in general since they are most often involved in some aspect of glycolysis, intermediary metabolism, or in the catalysis of certain general types of bonds (esterases, phosphatases, peptidases). Lack of representativeness is probably less serious for systematics, which has not confined itself to characters thought to be representative, than it is for genetic studies which attempt to estimate the total amount and kind of genetic variation in different kinds of organisms. In any event, the enzymes that are examined comprise a sufficiently large category to give meaningful information about many kinds of evolutionary changes.

A problem which is more critical for systematics is that, even for those enzymes examined, the redundancy of the genetic code means that only about 30% of the substitutions of nucleotides are expected to result in the substitution of amino acids that cause changes in electrophoretic mobility (Shaw, 1970). In addition, allozymes that have identical mobilities do not necessarily have identical amino acid sequences. In fact, recent studies utilizing amino acid sequencing (Boyer et al., 1972), heat denaturation (Bernstein et al., 1973; Singh et al., 1974), and variation in gel pore size (Johnson, 1976) suggest that a single mobility class on a gel may sometimes contain more than one enzyme. This requires that more weight be given to evidence of electrophoretic difference than to evidence of similarity. Additional biochemical tests, however, are available to determine whether allozymes with the same mobility have different amino acid sequences. All in all, electrophoretic evidence should be regarded as providing an underestimate of the actual amount of genetic difference between taxa.

Electrophoretic evidence does not include any information on the number of amino acid differences, or mutational steps, that cause differences in enzyme mobilities. A difference in mobility can reflect a single nucleotide substitution or numerous changes in nucleotide sequence. Thus, electrophoresis can demonstrate that two taxa have different allozymes of phosphoglucoisomerase, but it does not provide information about the amount of difference. This is likely to be greater with increasing phylogenetic distance.

Thus, the equation between phenotype and genotype remains acceptable even when the limitations of electrophoretic evidence are considered because they can be specified and the direction of bias is generally known.

ELECTROPHORETIC EVIDENCE: A FRAMEWORK FOR ANALYSIS

When tissue extracts are subjected to electrophoresis in a starch gel, the pattern of enzyme bands (number, spacing, and intensity) is an expression of the particular enzyme system assayed and its mode of inheritance. For some enzymes (usually esterases, phosphatases, and peroxidases), single individuals display complex patterns with as many as 10 to 15 bands because they possess numerous gene loci that code different molecular forms. In contrast, other enzymes are specified by a single structural gene and individuals might display only a single band following electrophoresis. The number of polypeptide subunits of each enzyme and the allelic state of the coding gene (homozygous or heterozygous) also determine the number of enzyme bands displayed. Thus, for an enzyme composed of a single polypeptide, an individual heterozygous at the coding gene displays two allozyme bands, but if the enzyme is dimeric (composed of two polypeptides), three allozymes are displayed, and if it is tetrameric, five are displayed (Fig. 1). In other cases, the polypeptide constituents of an enzyme are coded by different nonallelic genes, for example, alcohol dehydrogenase in maize (Freeling & Schwartz, 1973) and in sunflower (Torres, 1976), producing still additional variants.

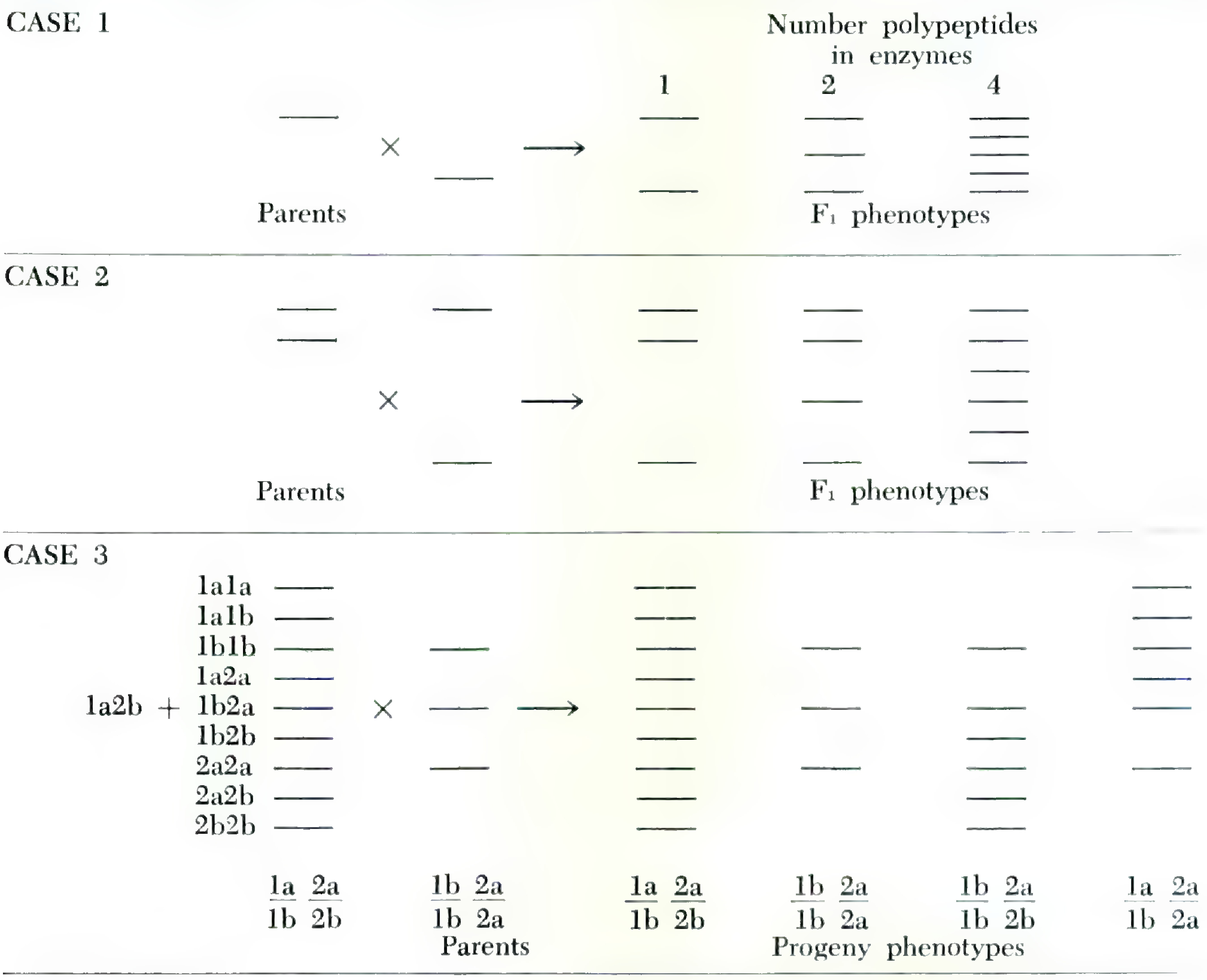
The number of enzyme bands can be reduced if enzymes specified by different genes overlap on the gel because they have similar mobilities, or if an individual is homozygous for a "null" allele (an absence of activity which genetic analysis demonstrates to be allelic to genes that specify active forms of the enzyme). Artifacts that might result from procedures of extraction or electrophoresis can also change band number. In addition to these biochemical factors, the pattern of enzyme bands displayed by different individuals in a population is a function of the amount of genetic variation for the enzyme system.

The presence of so many factors which influence the appearance of the electrophoretic phenotype means that the systematist must reject the temptation to compare electrophoretic data from different taxa by direct inspection, i.e., simply counting the number of bands with similar and dissimilar mobilities. Not only would this approach be biochemically faulty, but it nullifies several of the important advantages of electrophoresis, particularly the inference of enzyme homology, and the precise and quantifiable form of the evidence. The frequent complexity of the electrophoretic phenotype means that, at least for the complex systems that have a number of electrophoretically separable enzyme variants, a genetic analysis is necessary.

Such analysis demonstrates which variant forms of an enzyme system are specified by allelic genes and which by nonallelic genes; i.e., it distinguishes allozymes and isozymes. In addition, in many cases, it rules out the possibility of biochemical artifacts. Genetic analysis also leads directly to a quantitative specification of the electrophoretic data that usually is ordered as follows: the number of structural genes specifying the enzymes examined; the proportion of genes that show variation or, as the geneticist says, are polymorphic in that they have more than a single allele; the number of alleles per gene in the population; and the mean proportion of genes which is heterozygous per individual.

The protocol of formal genetic analysis can often be simplified with electro-

FIGURE 1. These diagrams present three examples of electrophoretic patterns in parents and their hybrids to illustrate that differences between individuals in the number of enzyme bands often do not equal the number of their genetic differences. Case 1 presents a cross between two individuals, homozygous for different alleles at a gene coding an enzyme. The number of bands per individual in their F_1 hybrids depends on the subunit structure of the enzyme. Note that for a dimeric enzyme, a heterozygous individual differs from each of its parents by two bands, but one allele; for a tetrameric enzyme, it differs from them by four bands, but one allele. Case 2 illustrates the same point but uses a cross between individuals homozygous for the same allele at one gene and homozygous for different alleles at a second gene. The F_1 phenotype depends on the subunit structure of the enzyme. In this example, polypeptides specified by the two genes do not have affinity for one another. Case 3 presents a cross between two individuals whose enzyme phenotype is also determined by two gene loci. In this case, the enzymes are considered to be dimeric, and polypeptides specified by both different alleles and different genes associate to form "hybrid" or heteromeric enzymes. The cross is a test cross between a double heterozygote and a double homozygote. If the genes assort independently, the four progeny classes are produced in equal numbers; if they are linked, the parental phenotypes are more frequent than the recombinant ones. Note that the double heterozygote differs from the double homozygote by six bands but only one allele at each gene. The polypeptide structure of each enzyme band is given on the left and the genotype of each individual is given below.



phoretic data because enzyme bands, with few exceptions, show codominant inheritance and segregate as single Mendelian factors (see reviews by Scandalios, 1969, 1974; Jacobs, 1975). This makes it possible to utilize progeny tests to replace formal crosses between individuals with different phenotypes, examine F_1 progeny phenotypes, and analyze phenotypic segregation patterns in the F_2

generation. In the progeny tests, individuals are grown from open-pollinated seeds collected on single plants in nature. Since these individuals all have one parent in common, they necessarily have in common its alleles. For many enzyme systems, study of the segregation pattern of the different variants in such progenies can indicate which of them are specified by allelic genes and which by different gene loci (Brown et al., 1975). However, for very complex systems in which several polymorphic genes and overlaps in the migration of different enzymes are involved, formal analysis is still required. Figure 1 presents examples of such analysis.

Before the introduction of the electrophoretic technique, the study of genetic variation in natural populations was unsatisfactory because it depended on the identification and enumeration of rare recessive mutants that, when homozygous, yielded visible morphological changes. The genetic basis of many of these characters is simple and clearly demonstrable, but they constitute only a very small proportion of the genetic variation in populations. The vast majority of phenotypic characters are apparently controlled by many genes each of which may have different individual effects. These so-called quantitative characters are also often strongly influenced by environmental variation. The result is that the contribution of individual genes of this type cannot be ascertained, and the extent to which they vary one from another in different individuals is undetectable. Thus, one studied either those rare characters controlled by one or two genes with major effects or the much more common characters controlled by many genes that are neither individually identifiable nor distinguishable from environmental influences. In consequence, the traditional methods of studying genetic variation were stymied by the impossibility of equating phenotypes with genotypes.

The electrophoretic procedure avoids most of these problems. In addition, it identifies genes which do not vary on the basis that their enzyme products do not vary in their electrophoretic mobility (within the limits mentioned in the previous section), making it possible to determine the proportion of genes that show variation. This advantage has been considered the "cornerstone" of the method (Hubby & Lewontin, 1966) because previously it was not possible to equate lack of variation with monomorphism at particular genes.

The determination of how many individuals and populations to sample before a confident statement can be made regarding the amount of genetic divergence between taxa is another important consideration in the use of electrophoretic evidence. A definition of the meaning of divergence greatly simplifies this problem. Thus, maximal divergence between two taxa at a gene locus means that they have no alleles in common. Minimal divergence at a gene locus means that the two taxa have similar complements of alleles in similar frequencies. Although the two extremes are connected by a wide variety of intermediate situations, the amount of divergence at a set of genes can often be fitted into a general picture. Thus, if a large number of genes is studied, about 30–50% of them are likely to be monomorphic, another 30–40% will be moderately polymorphic (two or three alleles), and the remaining genes will be highly polymorphic.

The distribution of genes in monomorphic and polymorphic categories permits the systematist to decide, at the outset of a study, the amount of sampling

necessary to test a given hypothesis. For example, at a polymorphic gene locus, an allele can be considered common (moderate to high frequency) and widespread, rare (less than 0.05) and widespread, common and local (one or two populations), or rare and local. For certain systematic purposes, one might decide that the first category is most relevant (it is the easiest to sample since alleles here have the highest probability of being included in a sample regardless of strategy). In logistic terms, this means that relatively little effort need be expended to find one more allele which is likely to have low frequency, be local in distribution, or both.

The number of individuals to sample per population is best viewed from the standpoint of how many plants to examine in order to have a 95% certainty of observing all the alleles at a locus which have frequencies greater than 0.05. This problem has been considered by Marshall & Brown (1975) who show that, even in the unlikely case of 20 alleles with frequencies of 0.05 each, a random sample of 120 gametes (60 individuals) will include, with 95% certainty, one copy of each allele. In sum, decisions related to sampling can be neatly bracketed because electrophoretic evidence consists of discrete and precise units of information.

A number of coefficients have been developed to summarize allele frequency data into a single figure that might be used to assess the degree of genetic divergence of taxa (Cavalli-Sforza & Edwards, 1967; Hedrick, 1971; Nei, 1972; Rogers, 1972); however, all of them appear to provide similar estimates (Avise, 1974). The data can also be used to construct dendrograms that cluster taxa according to their similarities (references in Avise, 1974). Another approach, described in the following section, that might be particularly useful for analysis of conspecific populations, makes use of the presence or absence of alleles rather than their frequencies (Gottlieb, 1975).

Electrophoretic Evidence: Applications

Electrophoretic analysis of enzyme variation provides efficient, quantitative estimates of the amount of genic variation within natural populations and the extent of genic divergence among populations. A very large number of electrophoretic studies have been made on animal species. The results appear remarkably consistent: (1) Single populations of both vertebrates and invertebrates contain substantial genetic variability, and perhaps as much as 90% of the total genetic information of their species (review in Powell, 1975; Selander, 1976); (2) Conspecific populations have a very high degree of genic identity (Nei, 1972), often with a mean above 0.90, on a scale of 0 to 1. Their high identity reflects the fact that the same allele is usually fixed at monomorphic genes (as much as 80 to 90% of the genes in vertebrates, for example), and, at the polymorphic genes, only the frequency of alleles differs (Avise, 1974); (3) Closely related species are considerably more differentiated than conspecific populations, with a mean genetic identity around 0.50 to 0.60, which suggests that different species of animals are almost completely distinct in allelic composition at about one-quarter to one-half of their genes (Ayala, 1975). Many of these differences may have evolved since their origins as species because much higher

values of genetic identity are observed for pairs of species which apparently originated in the Pleistocene (Nevo et al., 1974; Avise et al., 1975).

In contrast to the wealth of data for animal species, the number of electrophoretic studies of plant species is extremely small (fewer than a dozen groups of congeneric species have been examined for electrophoretic variation in a large number of enzymes) and, consequently, generalizations must still be considered tentative. The paucity of studies with plants is unfortunate because, in many ways, plants are better material than animals for electrophoretic investigations. Thus, they are often easy to grow in high numbers; they need not be killed to obtain a tissue sample so that individuals can be used for additional analysis; progeny-testing to establish the genetic control of enzyme variants is straightforward; natural populations are often spatially and ecologically delimited, permitting coordinated studies of ecological adaptations and amplitudes; phylogenies are often known unambiguously, facilitating analysis of the consequences of speciation; breeding systems are highly variable so that genetic consequences of different amounts of inbreeding can be studied directly and correlated with demographic inputs, etc.

The available electrophoretic studies with plants that are relevant to questions in systematics and evolution can be grouped into four major categories: (1) genetic divergence among conspecific populations; (2) genetic divergence among congeneric species, a subject which has also provided evidence of the genetic and biochemical consequences of speciation; (3) enzyme expression in diploid progenitors and polyploid derivatives; and (4) a heterogeneous group of special-purpose studies (not reviewed here because of space limitations) dealing with themes such as analysis of gene flow across species barriers (interspecific hybridization) (Chu & Oka, 1970; Levin, 1975), consequences of unusual chromosomal pairing mechanisms in *Oenothera* (Levy & Levin, 1975), demographic analysis (Schaal, 1975), the effect of breeding systems on the amount and expression of genetic variability (Allard, 1975; Allard & Kahler, 1971), and genetic diversity and edaphic specialization (Babbel & Selander, 1974).

Electrophoretic Evidence: Conspecific Populations

Electrophoretic variation in enzymes has been examined in natural populations (at least two) of about 28 plant species (Table 1). However, in many respects, the data is very uneven. For example, the number of enzyme systems examined and the number of genes that code them in the different species vary over a five-fold range. In addition, the choice of enzymes is diverse so that in some studies the proportion of genes specifying enzymes that are frequently highly polymorphic (esterases, phosphatases, peroxidases) is high, whereas in other studies many additional enzymes are included that are involved in basic metabolism (such as phosphoglucoisomerase, phosphoglucomutase, glutamate dehydrogenase, malate dehydrogenase, malic enzyme, glutamate oxaloacetate transaminase). Further, the number of populations sampled per species varies widely. The species themselves are nearly all annual but, in other respects, they are heterogeneous including diploids and polyploids, obligate outcrossers and pre-

TABLE 1. Electrophoretic variation for genes specifying enzymes and genetic identities (calculated with the statistic of Nei, 1972) of conspecific plant populations. The data presented are for each species treated as a whole. The species list includes only species in which a large number of enzymes was analyzed in at least two populations.

Species	No. Pop.	No. Enzyme Systems/ No. Genes	% Genes Polymorphic	Mean No. Alleles/ Polym. Gene	Mean Heterozygosity	Genetic Identity	Reference
Avena barbata "I"[a]	9	3/5	0.00	—	0.00	1.00	Clegg & Allard, 1972
A. barbata "II"[a]	7	3/5	1.00	2.00	0.03	0.54	Clegg & Allard, 1972
Clarkia biloba[b]	3	7/8	0.62	3.60	0.15	0.92	Gottlieb, 1974a
C. lingulata[b]	2	7/8	0.62	3.33	0.07	0.90	Gottlieb, 1974a
C. rubicunda[b]	4	8/11	0.64	2.00	0.11	—	Gottlieb, 1973a
Gaura longiflora[c]	3	10/18	0.33	3.16	0.07	0.99	Gottlieb & Pilz, 1976
G. demareei[c]	2	10/18	0.28	3.00	0.05	0.99	Gottlieb & Pilz, 1976
Hymenopappus scabrosaeus[b]	14	6/7	0.71	2.12	0.20	0.97	Babbel & Selander, 1974
H. artemisiaefolius[b]	12	6/7	0.71	2.05	0.21	0.94	Babbel & Selander, 1974
Lupinus subcarnosus[b]	8	7/8	0.88	1.84	0.10	0.97	Babbel & Selander, 1974
L. texensis[b]	10	7/8	0.88	3.12	0.36	0.96	Babbel & Selander, 1974
Lycopersicon cheesmanii[a]	54*	4/14	0.57	2.65	0.01	—	Rick & Fobes, 1975
L. chmielewski[b]	8*	4/14	0.50	3.52	—	—	Rick et al., 1976
L. parviflorum[a]	8*	4/14	0.14	2.00	0.00	—	Rick et al., 1976
Lycopodium lucidulum[a]	16	11/18	0.28	1.39	0.07	0.98	Levin & Crepet, 1973
Oenothera biennis[a]	106*	11/20	0.30	1.40	0.10	0.95	Levy & Levin, 1975
O. parviflora[a]	29*	11/20	0.40	1.55	0.15	0.92	Levy & Levin, 1975
O. strigosa[a]	29*	11/20	0.25	1.30	0.03	0.97	Levy & Levin, 1975
Phlox cuspidata[a]	10	11/16	0.38	2.33	0.01	0.95	Levin, 1975
P. drummondii[c]	10	11/16	0.25	2.25	0.04	0.97	Levin, 1975
Silene maritima[b]	2	13/21	0.29	2.33	~0.14	—	Baker et al., 1975
Stephanomeria exigua subsp. *carotifera*[c]	11	8/14	0.57	4.80	0.09	0.98	Gottlieb, 1975
S. exigua subsp. *macrocarpa*[a]	5	8/14	0.07	2.00	< .01	0.99	Gottlieb, unpublished
S. paniculata[a]	5	14/25	0.04	2.00	0.00	0.99	Gottlieb, unpublished
Tragopogon dubius[a]	6	13/21	0.24	2.50	<0.01	0.97	Roose & Gottlieb, 1976
T. porrifolius[a]	3	13/21	0.10	2.00	<0.01	0.98	Roose & Gottlieb, 1976
T. pratensis[a]	3	13/21	0.00	—	0.00	1.00	Roose & Gottlieb, 1976
T. mirus[a]	6	13/21	0.24	1.20	++**	—	Roose & Gottlieb, 1976
T. miscellus[a]	5	13/21	0.19	2.00	++**	—	Roose & Gottlieb, 1976

[a] Highly self-pollinating.
[b] Self-compatible.
[c] Self-incompatible.
* Strains or accessions.
** Tetraploid species with 40% phenotypic heterozygosity; see text.

dominant selfers, and recently evolved and ancient taxa. However, in spite of these disparities, two results appear well established.

First, the amount of genetic variability within plant populations is closely correlated with their breeding systems (Table 1). Thus, the mean number of alleles per polymorphic gene averages 1.88 ± 0.12 for highly self-pollinating species and 2.86 ± 0.24 for outcrossing ones. The mean proportion of genes that is heterozygous per individual follows suit: 0.032 ± 0.013 for selfers and 0.133 ± 0.026 for outcrossers. These results indicate that breeding system influences not only the degree of genetic homozygosity but also the total amount of variability that can be maintained in plant populations.

Second, conspecific plant populations are extremely similar genetically as demonstrated by their very high mean genetic identity $\bar{I} = 0.95 \pm 0.02$, averaged over all species (Table 1). This is an important result for systematics because it suggests that electrophoretic evidence from one or a few populations very often constitutes an adequate sample of an entire species.

The very high degree of genetic similarity among conspecific populations leads to the suggestion that should populations be discovered which have novel alleles or distinct allele frequencies at more than a few gene loci, such populations are very likely to constitute distinct taxa and should be further examined with this in mind. Such evidence has already been used to identify a subspecies of *Drosophila willistoni* (Ayala, 1973) and a new species of sea cucumber (Manwell & Baker, 1963). It is not unlikely that electrophoretic evidence will also be similarly used to identify hitherto unrecognized plant species.

An approach to the comparison of conspecific populations that considers the representativeness of single populations rather than their identity to one another has also been proposed (Gottlieb, 1975). Designated the Complement Index, it compares the number of nonunique and nonubiquitous alleles (present in more than one but not all populations) in each population with the total number of such alleles identified in all the populations examined. Since the presence of alleles increases the biochemical repertoire of a population, the number of alleles constitutes a very good and easily obtained estimator of the relative potential of different populations for adaptive evolutionary change. The Complement Index would be particularly useful for taxa in which populations contain large numbers of different low frequency alleles, a situation that may be common in outcrossing plants. Thus, 11 populations of *Stephanomeria exigua* subsp. *carotifera* all possessed the same gene at 6 monomorphic loci and 13 high frequency alleles at 8 polymorphic ones, but different numbers of 25 other low frequency alleles (Gottlieb, 1975). Calculation of the Complement Index showed that the populations actually represented subsp. *carotifera* to very different degrees even though they had a mean genetic identity, $\bar{I} = 0.98$ (Gottlieb, 1975). The average population had only about half of all the genes identified in the subspecies as a whole; nevertheless, one of them possessed every one of the nonunique alleles. This population contained more of the genetic resources of subsp. *carotifera* than any other and is the most likely to persist through environmental fluctuations. In addition to identifying such populations (which, with cultivated plants have obvious importance for germ plasm conservation), the Complement

Index could be used to compare the representativeness of populations of different taxa.

Electrophoretic Evidence: Congeneric Species

The large amount of electrophoretic variation in natural populations of plants initially led systematists to presume that extensive surveys within and between populations were required in order to use electrophoretic evidence for meaningful systematic comparisons between species (Turner, 1969). This point of view apparently took hold because genetic studies had only rarely been carried out and therefore it was difficult, if not impossible, to make sense of the complex banding patterns that were observed (many of the early studies unwittingly utilized esterases and peroxidases which are the most difficult systems to interpret). The absence of genetic data and the small number of populations that had been sampled combined to give the impression that the polymorphisms inherent in electrophoretic evidence lessened its value for systematics.

However, now it is realized that once polymorphisms are defined in genetic terms so that "bands" can be equated with alleles and different gene loci, then their presence actually increases the power of electrophoretic evidence for systematic studies since they reveal to a large degree the accumulated record of numerous mutations that have become established in the coding genes. In addition, extensive sampling of conspecific populations is often not necessary for species comparisons because many of the alleles, particularly those with frequencies above 0.20, as well as the genes at monomorphic loci, are now known to be present in most, if not all, populations of a species. However, although the number of populations sampled can be reduced, it remains important to increase the number of enzymes sampled. This would tend to lessen the effect of biases that might result from selecting only enzymes likely to be polymorphic or those limited to any particular biochemical category.

About a dozen studies have been made that provide evidence of the extent of genetic divergence between congeneric species (Table 2). These studies show that most pairs of species have strikingly reduced genetic identities; $\bar{I} = 0.67 \pm 0.07$, averaged over all pairs of species examined. A number of species pairs, however, have very high genetic identities, within the range of those characteristic of conspecific populations. For three of these cases, *Stephanomeria exigua* subsp. *coronaria* and "Malheurensis" (Gottlieb, 1973b, 1976), *Clarkia biloba* and *C. lingulata* (Gottlieb, 1974a), and *Gaura longiflora* and *G. demareei* (Gottlieb & Pilz, 1976), the species are known to be related as progenitor and derivative, respectively, with the derivative being of relatively recent origin.

The three cases represent the three possible pathways of diploid speciation in annual plants, defined in terms of the breeding systems: self-incompatible to self-compatible, self-compatible to self-compatible, and self-incompatible to self-incompatible, respectively. A fourth example of very high genetic similarity between progenitor and derivative diploid species has recently been identified in *Lycopersicon* (Rick et al., 1976). The lack of genetic divergence between the members of each species pair indicates that, shortly after their origin, annual plants, regardless of their breeding system, are still limited genetic versions of

TABLE 2. Nei's (1972) mean genetic identity, $\bar{I}$, between pairs of populations of congeneric plant species.

Species	$\bar{I}$	Reference
Clarkia biloba × *C. lingulata*	0.88	Gottlieb, 1974a
Clarkia rubicunda × *C. franciscana*	0.28	Gottlieb, 1973a
Gaura longiflora × *G. demareei*	0.99	Gottlieb & Pilz, 1976
Hymenopappus scabrosaeus × *H. artemisiaefolius*	0.90	Babbel & Selander, 1974
Lupinus texensis × *L. subcarnosus*	0.35	Babbel & Selander, 1974
Oenothera strigosa × *O. biennis*	0.97	Levy & Levin, 1975
Oenothera strigosa × *O. parviflora*	0.54	Levy & Levin, 1975
Oenothera biennis × *O. parviflora*	0.55	Levy & Levin, 1975
Phlox drummondii × *P. cuspidata*	0.67	Levin, 1975
Stephanomeria exigua subsp. *coronaria* × "Malheurensis"	0.94	Gottlieb, 1973b, 1976
Tragopogon dubius × *T. porrifolius*	0.50	Roose & Gottlieb, 1976
Tragopogon dubius × *T. pratensis*	0.62	Roose & Gottlieb, 1976
Tragopogon porrifolius × *T. pratensis*	0.53	Roose & Gottlieb, 1976

their progenitors and possess very few or no unique alleles insofar as their genomes have been assayed. The species are extracted from the parental repertoire of phenotypic variation and genetic polymorphisms. Thus, the speciation process does not seem to involve early reconstitution of the genome of the derivative species, even though it may possess certain unique morphological traits or other features (Gottlieb, 1976).

The other two examples of high genetic identity between species are not inconsistent with this thinking. Thus, the similarity of *Oenothera strigosa* and *O. biennis* presumably reflects the fact that they have one genome in common (Levy & Levin, 1975). And the high identity of the two species of *Hymenopappus* is concordant with their very close phylogenetic relationship as judged by their high overall morphological similarity; they were maintained as species because they apparently do not hybridize despite extensive parapatric contact (Turner, 1956). However, it is not clear if the results with annual plants will also characterize perennial plant species. This is because perennials, especially long-lived ones, appear to evolve gradually, rather than rapidly and abruptly, and they are more likely to be reproductively isolated by ecological and pollination factors rather than hybrid sterility resulting from chromosomal restructuring.

Electrophoretic evidence has also been used to show that species which appear similar may actually not be so. Thus, *Clarkia franciscana*, a highly self-pollinating species thought to have evolved by rapid reorganization of chromosomes from the morphologically similar *C. rubicunda* (Lewis & Raven, 1958), is totally divergent from that species in a high proportion of its genes (those coding six of the eight enzyme systems assayed) (Gottlieb, 1973a). In addition, *C. franciscana* has a duplicated gene for alcohol dehydrogenase which further distinguishes it from *C. rubicunda* (Gottlieb, 1974b). Such marked genetic differentiation requires that the phylogenetic separation of the two species occurred much longer ago than had been presumed, and makes its proposed mode of origin quite uncertain. Therefore, a reasonable criterion to apply in cases like

this is that a species not be accepted as having originated recently from another extant species if it is not electrophoretically highly similar to its putative parent (Gottlieb, 1973a). This criterion has now been satisfied in the four examples described above.

When additional electrophoretic studies are reported, it may very well turn out that such evidence reflects species divergence more sensitively than other types of biochemical analysis. Thus, two-dimensional chromatography of certain flavonoids in *Tragopogon dubius*, *T. porrifolius*, and *T. pratensis*, failed to distinguish a single component that was species-specific (Brehm & Ownbey, 1965), even though the morphological differences between these species are "broad, sharp and absolute" (Ownbey, 1950). But, electrophoretic analysis of many enzymes in North American populations of the three Tragopogons revealed very clearly that they were fixed for different alleles at about 40% of the 21 genes examined (Roose & Gottlieb, 1976). Other groups of plants have not yet been studied so extensively both for electrophoretic variation in enzymes and chromatographic variation in flavonoids and, therefore, it is not possible to know if such a result will prove general. However, this is not implausible since changes in the amino acid sequences of a large number of polypeptides which affect electrophoretic mobilities of enzymes are more likely to reflect early stages of genetic divergence than are changes in secondary metabolites such as flavonoids which are products of enzyme-catalyzed biosyntheses.

Electrophoretic evidence is also likely to be useful in other systematic investigations which require knowledge of the extent of genetic similarity of closely related diploid species. An attractive use will be to examine cases in which one species appears to be a stabilized derivative of hybridization between two other extant species such as *Lasthenia burkei* (Ornduff, 1976), *Potentilla glandulosa* subsp. *hansenii* (Clausen et al., 1940), *Achillea rosea-alba* (Ehrendorfer, 1959), and *Delphinium gypsophilum* (Lewis & Epling, 1959). Another use will be to answer a novel systematic question having to do with the relative similarity of species in different genera. A sample question might be: Are species of *Clarkia* more similar to one another than species of *Baptisia*? Once again the question becomes plausible because of enzyme homology and because electrophoretic evidence is composed of discrete, quantifiable units of information. The comparison of relative taxonomic distance in different genera might eventually lead to the development of procedures to standardize certain taxonomic decisions.

A further application of electrophoretic evidence above the species level takes advantage of its ability to distinguish species with different numbers of genes specifying the same enzyme system. In cases where an enzyme is composed of several polypeptides, the formation of "hybrid" enzymes by the association of subunits coded by different gene loci provides strong evidence for their homology and the origin of one of the genes through duplication. Clearcut examples of such gene duplication have been documented for animal lactate dehydrogenase (reviewed in Markert et al., 1975), hemoglobins (Ingram, 1961), and phosphoglucoisomerase (Avise & Kitto, 1973). Gene duplication is very probably a unique event in the evolutionary history of organisms and, therefore, it can provide evidence of the monophyletic origin of large groups of species and genera.

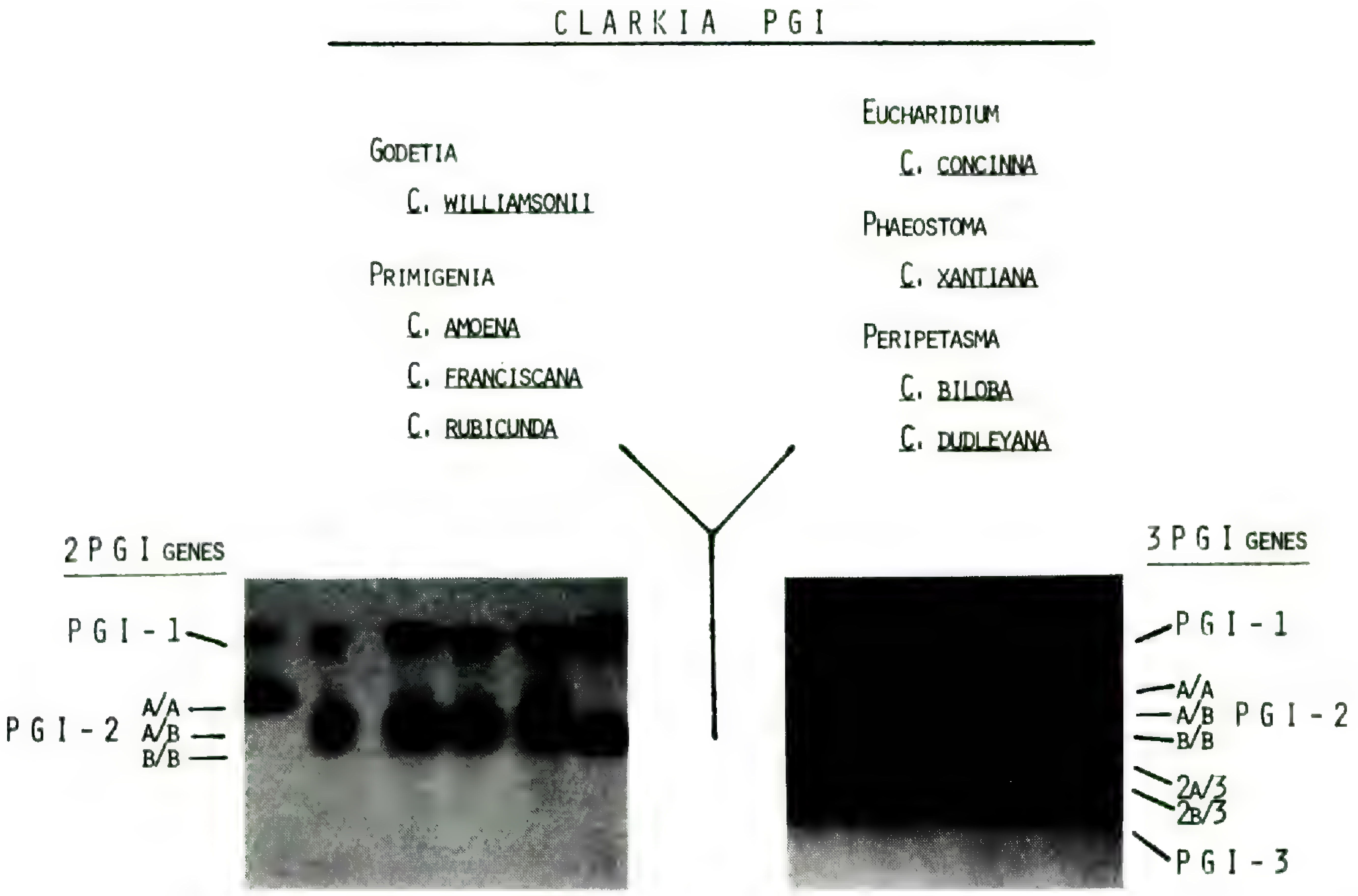


FIG. 2. Eight diploid species in five of the seven diploid sections of *Clarkia* which have been examined to date can be divided into two groups on the basis of the number of genes they have specifying phosphoglucoisomerase subunits. The photographs show typical electrophoretic phenotypes for this enzyme system in the two groups. Details of the genetic analysis are described by Gottlieb (1977).

During studies of the genetic divergence of diploid species of *Clarkia*, I uncovered two cases of apparent gene duplication (Gottlieb, 1974b, 1977). The one involving duplicated phosphoglucoisomerase (PGI) is particularly relevant to systematic studies because it tests directly the taxonomic delimitation of sections within the genus proposed by Lewis & Lewis (1955). Genetic analysis of PGI in *Clarkia* has shown that species either have two or three genes specifying these enzymes (Gottlieb, 1976, 1977). To date, eight species in five of the seven diploid sections of the genus have been examined: *Clarkia rubicunda*, *C. amoena*, and *C. franciscana* in the presumed primitive section *Primigenia* have two genes (Gottlieb, 1973a) as does *C. williamsonii* in the *Godetia* section (Price, 1975). Section *Phaeostoma* is represented by *C. xantiana*, *Peripetasma* by *C. biloba* and *C. dudleyana*, and *Eucharidium* by *C. concinna*, and all of these species have three PGI genes (Gottlieb, 1977) (Fig. 2).

The duplication was originally recognized because individuals from species with three PGI genes display more enzymes upon electrophoresis than those from species with two PGI genes. The actual number of enzyme bands observed depends on the allelic state of the coding genes and the affinity of polypeptides specified by the different alleles and the different gene loci. PGI is composed of two polypeptides so that an individual heterozygous for different alleles at a single coding locus normally produces three enzymes by two-by-two association of the two polypeptides (aa, bb, ab). In the Clarkias examined, the

gene coding the most anodal PGI appears to be invariant since individuals with either two or three PGI genes have always possessed a single fast PGI; polypeptides specified by this gene, called *PGI-1*, do not form a "hybrid" enzyme with those specified by either of the other genes (Fig. 2).

Thus, the maximum number of PGI enzymes observed in the two-gene species was four (the single fast PGI coded by *PGI-1* plus three enzymes in individuals heterozygous at *PGI-2*). However, as many as ten enzymes have been observed in the three-gene species because polypeptides specified by the duplicated gene, called *PGI-3*, from "hybrid" enzymes with those specified by the original *PGI-2* gene. Thus, when both *PGI-2* and *PGI-3* are heterozygous, four different polypeptides are made which aggregate to form nine distinguishable enzymes (Fig. 1, case 3), and *PGI-1* codes a tenth enzyme band.

The duplication is thought to have originated by the generation of a duplicated chromosome segment in a progeny of a cross between individuals differing for chromosomal rearrangements, possibly a partially overlapping reciprocal translocation (reviewed in Burnham, 1962). Self-fertilization would make the segment homozygous in a few generations. This mode of duplication is likely in *Clarkia* because in this genus, species are self-compatible and differ by large numbers of reciprocal translocations. Such duplications will not be linked; recent genetic analysis (Gottlieb, 1977) in *Clarkia xantiana* has shown that *PGI-2* and *PGI-3* assort independently, which is consistent with the proposed duplication process.

The species with three PGI genes can be considered a monophyletic group that traces back to an ancestor that branched away from the *Primigenia-Godetia* stock. That two genes is the ancestral number is directly supported by the observation that *Oenothera*, the most closely related genus to *Clarkia*, also has two genes for PGI (Levy et al., 1975) as does *Gaura* (Gottlieb & Pilz, 1976), another genus in the same tribe of the Onagraceae. The utilization of the number of genes coding specific enzymes to classify groups of species into monophyletic assemblages appears not to have a parallel in current systematic research. Gene duplication provides a strict homology, absent with most morphological characters, because convergence in particular structural genes is highly improbable since it would require a very high number of mutational changes to alter the coding properties of a different nonhomologous locus.

Electrophoretic Evidence: Polyploid Species

The ancestry of most allotetraploid species (tetraploids are used as an example of polyploids) can, in principle, be traced back to a chromosome doubling in a diploid individual which was produced by hybridization between differentially adapted populations. The initial allelic composition of the tetraploid plants is a direct function of the degree of genetic divergence of the diploid progenitor populations and is likely to be substantially greater if these represent species. This follows because species have a very much higher probability than conspecific populations of possessing different alleles at their monomorphic gene loci and nonoverlapping complements of alleles at polymorphic genes. After the events of its origin, the courses of evolution in the tetraploid and its diploid

parents are independent which suggests that the more ancient the tetraploid, the less likely will it retain the alleles it inherited in an unmutated state, and, likewise, alleles will continue to evolve in the diploids. Thus, the ability to identify the diploid parents of a tetraploid species with electrophoretic evidence depends on numerous factors having to do with the amount of divergence of the diploids at the time of tetraploid origin as well as subsequent evolutionary events.

It follows that evidence brought to bear on the phylogeny of a tetraploid species not be limited to a few enzymes or to a limited class of proteins, and that particular attention be paid to specific protein homology and the mode of inheritance of the proteins examined in order that an absence or difference in mobility can be interpreted in terms of genetic changes. This prescription has been ignored in numerous studies of diploid and tetraploid plant species which have employed only one or two enzyme systems or have sampled only seed proteins and, consequently, many of these studies have uncertain value and are not dealt with here.

In general, electrophoretic analysis has demonstrated that polyploid species express, additively, enzymes present separately in their diploid parents. This result has been reported, for example, in wheat (Hart, 1969; Mitra & Bhatia, 1971; Barber, 1970), cotton (Cherry et al., 1972), *Nicotiana* (Smith et al., 1970; Reddy & Garber, 1971; Sheen, 1972), *Phaseolus* (Garber, 1974), *Stephanomeria* (Gottlieb, 1973c), and *Tragopogon* (Roose & Gottlieb, 1976). If the duplicated genes of polyploids specify different polypeptide subunits of multimeric enzymes (those that are composed of more than one polypeptide), additional "hybrid" enzymes are produced which are not expressed in a diploid parent if it lacks both coding alleles. For many enzymes, the polyploid species is a "fixed heterozygote" because all of its individuals express a multiple enzyme phenotype that reflects their possession of different coding alleles inherited from the diploid species. This multiple enzyme phenotype does not exhibit genetic segregation because, at meiosis, chromosome homologues often pair preferentially so that genes inherited from both diploid parents go to the same pole and each gamete receives one copy of each of them. At fertilization, each gene is made homozygous, but their presence in duplicate means that a heterozygous (multi-enzyme) phenotype can be produced in the tetraploid. The multiplicity of enzymes in a polyploid species may extend the range of environments in which normal development can take place, and this is a reasonable hypothesis to account for the frequent wider distribution of tetraploid species relative to the diploids in many genera (Barber, 1970; Manwell & Baker, 1970; Gottlieb, 1976).

The general observation that the enzymes usually assessed by electrophoresis are expressed additively in polyploid species (the only apparent exception is a study in wheat, Sing & Brewer, 1969) may reflect, to some extent, the relatively recent origin of the tetraploids which have been examined. Although ancient polyploid complexes have not yet been studied by electrophoresis, many recently evolved polyploids have considerable systematic and evolutionary significance because they provide critical evidence regarding the initial genetic and biochemical consequences of this type of genome doubling.

The most extensive comparison of enzyme variation in diploid and tetraploid

species has been made in *Tragopogon* (Roose & Gottlieb, 1976). The three diploid species, *T. dubius*, *T. porrifolius*, and *T. pratensis*, were introduced to America from Europe during recent times. They are sharply delimited morphologically without overlap in a number of characters (Ownbey, 1950). In southeastern Washington and adjacent Idaho, Ownbey (1950) discovered that interspecific hybridization between them had given rise to two different tetraploid species: *T. dubius* and *T. porrifolius* were the parents of *T. mirus*, and *T. dubius* and *T. pratensis* were the parents of *T. miscellus*. These two tetraploid species represent the only unambiguous examples of the very recent natural origin of polyploid species.

Electrophoretic evidence revealed that the three diploid species in North America are completely divergent (monomorphic for different alleles) at about 40% of the 21 genes that were examined, a result fully concordant with their morphological differentiation. The tetraploids inherited both alleles at each of these genes: *T. mirus* expresses an additive pattern for nine genes and *T. miscellus* for seven genes, including five in common with *T. mirus*. In both tetraploids, the additive pattern includes novel hybrid enzymes not produced in the diploid species. Each of the enzyme phenotypes in the tetraploids was fully accounted for by simple additivity of the polypeptides specified by genes inherited from its respective diploid parents. The observed patterns fully confirmed the ancestry of both tetraploids which was proposed by Ownbey (1950). These results, as well as others, clearly indicate that electrophoretic analysis of large numbers of enzymes can be an extremely useful and precise probe to identify diploid progenitors of polyploid species.

In summary, electrophoretic evidence can be used to test many different types of hypotheses regarding genetic divergence that have already been generated in plant systematics. In addition, its unique perspective will probably help to link questions previously considered to require only systematic or evolutionary evidence to different sources of evidence in biochemistry and plant development.

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THE APPLICATIONS OF MOLECULAR EVOLUTION TO SYSTEMATICS: RATES, REGULATION, AND THE ROLE OF NATURAL SELECTION[1]

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The development of biochemical methods for comparing the amino acid sequences of homologous proteins from different species has provided a powerful tool for investigations of evolution and systematics. Perhaps the most intriguing (and most controversial) result of the comparative studies of proteins using these methods has been the discovery that sequences may change at nearly constant rates (Wilson, Carlson & White, 1977). This is not to imply that different genes or proteins evolve at the same rate: rather, each class of proteins has its own characteristic rate (Dickerson, 1971). (Serum albumin, for example, has evolved more rapidly than cytochrome *c*, but serum albumin has evolved at approximately the same rate among all species of mammals tested, as has cytochrome *c*.) The degree of rate constancy has been the subject of intense debate, but the most current evidence indicates that the variation in evolutionary rate for a given protein is only about twice the variation expected for a totally stochastic process such as radioactive decay (Fitch, 1976). Within these limits, then, a given macromolecular sequence may be used as an evolutionary "clock."

The empirical discovery that molecules can be evolutionary "clocks" has been applied to a variety of problems in evolution and systematics. Most frequently, sequence data for a given protein from a number of species has been used to reconstruct phylogenetic trees depicting the probable order of branching of the lineages leading to modern species from a common ancestor. For example, Boulter and his colleagues have reconstructed a possible phylogeny for the flowering plants based on the cytochrome *c*, plastocyanin, and ferredoxin sequences of representative species (Boulter, 1974). In addition, phylogenetic analysis of sequences of 5S and 16S ribosomal RNA from chloroplasts, bacteria, blue-green algae, and cytoplasm of green plants has confirmed that chloroplasts evolved from photosynthetic prokaryotes living as endosymbionts within the cytoplasms of primitive heterotrophic plants (Margulis, 1970; Bonen & Doolittle, 1976; Zablen et al., 1975; Hori, 1975).

Molecular phylogenies may also indicate evolutionary times of divergence if the divergence time for at least one branching event in a tree can be accurately estimated from paleontological or biogeographical evidence. The use of cytochrome *c* sequences to estimate times of divergence for flowering plants poses a fascinating, and still unresolved dilemma. If the cytochromes *c* of plants are evolving at the same rate as those of vertebrates, which have a unit evolutionary period of about 20 million years, then the intraordinal divergence times for flower-

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ing plants would be about 240 million years ago (Ramshaw et al., 1972; Boulter et al., 1972). Since the first clearly authentic fossils of flowering plants occur about 130 million years ago (Sporne, 1971), an alternative interpretation of the data is that morphologically plant cytochromes *c* have evolved twice as fast as those of vertebrates (Cronquist, 1976). Workers in this field are now giving serious attention to the possibility that the origin of flowering plants is more ancient than is indicated by the available fossil evidence (Wilson, Carlson & White, 1977). This situation may be analogous with the origin of mammals, in that the group is very ancient, while adaptive radiation within the group is more recent.

The molecular evolutionary approach may also have revealed an important mechanism for evolution at the organismal level. This discovery results from the observed discrepancy between the evolution of macromolecules and the evolution of organisms. The comparison of humans and chimpanzees at both the macromolecular level and organismal levels indicates that the two species differ to an extent considered familial in morphology, behavior, and adaptive strategy, while their protein sequences differ by less than one percent—a level of difference characteristic of sibling species of *Drosophilia* or mammals (King & Wilson, 1975). Major adaptive changes may thus be based on molecular events other than sequence changes in structural genes. What sorts of events might these be? Experimental studies of bacterial evolution have demonstrated that major phenotypic changes—in the bacterial case the acquisition of a new metabolic activity—depend on an increase in the effective concentration of a protein which previously limited the rate of metabolism of a given substrate, rather than on a qualitative change in the substrate specificity of any protein (Lerner et al., 1964). These quantitative effects could be due to point mutations in regulatory genes or to chromosomal rearrangements such as duplications and translocations (Wilson, 1975). The observation that rates of karyotypic change are fastest in vertebrate groups with the most rapid phenotypic evolution may indicate that major adaptive shifts in the evolution of multicellular organisms are frequently associated with chromosomal rearrangements (Wilson et al., 1975).

The independence of the evolution of organisms and the evolution of their structural genes may provide a new perspective for investigating the evolutionary roles of natural selection versus random fixiation of selectively neutral alleles. If the random fixation of neutral substitutions were principally responsible for sequence evolution of genes and proteins, it would follow that the rate of sequence evolution would depend primarily on the mutation rate, which is assumed to be constant with time. The "neutral" hypothesis is thus consistent with the observation that sequence evolution depends on calendar time. In addition, the "neutral" hypothesis accounts for the observation that proteins can differ greatly in sequence without differing appreciably in biological activity. At the same time, it is unequivocably established that natural selection acts at the level of the organism, and that this selective pressure varies greatly over time and space. It is tempting to suggest a hypothesis consistent with—though in no way proven by—each of these observations: that fixed substitutions in the variable regions of structural genes have generally not been subject to selective

pressures, since these substitutions are largely irrelevant to the adaptive success of the organism. Instead, natural selection at the level of the organism may be reflected at the molecular level in both rapid elimination of deleterious mutations in regulatory systems and fixation of occasional adaptive changes in loci or patterns of genome organization controlling the expression of structural genes.

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CHEMOSYSTEMATICS—ANALYSES OF POPULATIONAL DIFFERENTIATION AND VARIABILITY OF ANCESTRAL AND RECENT POPULATIONS OF *JUNIPERUS ASHEI*[1]

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ABSTRACT

Three types of data were used to analyze 28 natural populations of *Juniperus ashei*: 16 morphological characters, 152 terpenoids, and 23 peroxidases. In this paper the peroxidase electromorphs were treated as ordinary qualitative chemical characters to examine the feasibility of using isozymes for taxonomic purposes and as indicators of populational variability. The data sets were subjected to various numerical analyses to examine regional trends, ancestral affinities, and variability within populations. Principal coordinate analysis was used to resolve the major coordinates of variation from the similarity matrix of each data set. Coordinate loadings were then contoured for the first three coordinates of each similarity matrix to aid the visualization of the regional trends. The terpenoids and morphology showed a series of uniform populations from central Texas into the Ozarks with divergent populations on the south and west portions of the range, extending into northern Mexico. No regional trends were apparent in the peroxidases and no corresponding modes of variation were seen between the peroxidases and the other two data sets. Pleistocene vegetation is reviewed and migration paths are speculated upon. Advanced and primitive character states are discussed. The uniform body of *J. ashei* populations from central Texas to the Ozarks appear to be advanced (recent), whereas the divergent populations seem to be more primitive (ancestral). A method called differential similarities is introduced to analyze the clinal gradation of *J. ashei* toward *J. saltillensis* in Mexico. Intrapopulational variability was analyzed by use of the average similarity within populations and the coefficient of phenetic variation (CPV). In general, the recent populations had high similarities and low variability, and the ancestral populations had lower average similarities and higher CPVs with both the morphological and terpenoid data. The pattern of variation in the peroxidases could not be generalized upon, but appeared to be mosaic. Peroxidases did not appear useful in this analysis when subjected to standard numerical analysis procedures. The evolution of *J. ashei* into its present distribution appears to have had at least two phases composed of very uniform, recent migrations and persistent, variable, relict populations perhaps extending close to the geographic origin of this taxon in northern Mexico.

The use of chemical characters has gained widespread acceptance during the past decade to the point that a graduate student thesis in systematics is now unusual if no chemical data are utilized. Because of the relative ease of use, flavonoids are widely utilized in systematic and evolutionary plant studies. The early works on *Asplenium* (Smith & Levin, 1963), *Lemnaceae* (McClure & Alston, 1966) and *Baptisia* (Alston & Turner, 1963) are classics, required reading for chemosystematic students. Likewise, classic is the work on betalains by Mabry and coworkers (summarized in this symposium). Whereas flavonoids and betalains have been extensively used above the species level (probably due to the qualitative nature of the methods), terpenoids, due to the quantitative nature of gas/liquid chromatography, have been more widely used at or below

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the species level. The gymnosperms have been the focus of many studies of populational differentiation which have uncovered clines (Flake et al., 1969, 1973), chemical races (Smith et al., 1969), hybridization (see von Rudloff, 1975 for an excellent review), and ancestral migrations (Adams, 1975a; Zavarin & Snajberk, 1973). In the angiosperms, work on the monterpenes of *Bursera* (Mooney & Emboden, 1968) demonstrated the use of these compounds in the detection of clinal variation. Of course, the work on the Australian *Eucalyptus* species has been of tremendous use in the classification of populations of these taxa and is well known.

Although studies using terpenoid characters to analyze populational differentiation are well known, the analysis of population variability in relation to important population biology questions such as the founder's effect, genetic drift, the effects of small versus large populations and central versus peripheral sites on variability have not been addressed. The relatively recent rise in the use of isoenzyme data has rekindled an interest in the examination of these questions. Gottlieb (at this symposium) has reviewed the literature on isozymes and their use in systematics. Nevertheless, it seems in order to mention that the "isozyme bandwagon" has become the current fad before we have developed a very thorough knowledge about the molecular basis of the electromorphs distinguished on gels.

Before the widespread use of isozymes, the study of variability within populations seems to have stagnated with the exception of the numerical taxonomic school (including morphometrics). Gilmartin (1969a, 1969b, 1974, 1976) has introduced a new idea called the coefficient of phentic variation (CPV) to examine the combined effects of many characters on variability. The CPV is merely the standard deviation of the mean similarity among a group of operational taxonomic units (OTUs) divided by that mean similarity. Whereas the mean similarity of a group tells about the average affinities, the CPV shows how homogeneous are the similarities of one group versus another group. Since the CPV is normalized by the mean similarity, different character sets can be compared as well as different levels of organization (i.e., population vs. species vs. genus). To my knowledge, the CPVs have not been used to study population variability with the exception of the studies by Gilmartin. The purpose of this paper is to examine population differentiation and variability in *Juniperus ashei* Buch. using three contrasting sets of characters: morphological characters, volatile terpenoids from leaves, and leaf peroxidases. The literature on *J. ashei* has been reviewed by Adams & Turner (1970).

Juniperus ashei is a taxon of a rather restricted range, occurring on limestone outcrops from northern Mexico to southern Missouri (Fig. 1). The Edwards Plateau region of central Texas supports dense populations covering thousands of acres, whereas the disjunct populations (Lubbock-Post, Texarkana, Arbuckle Mountains, Ozark Mountains, and northern Mexico) often have nearly pure stands of *J. ashei*, but seldom cover such large areas. Being a fairly conspicuous conifer tree, one can be relatively confident in the taxonomic distribution records which imply that there are few, if any, trees between the disjunct populations and the Edwards Plateau populations. Thus, this would appear to

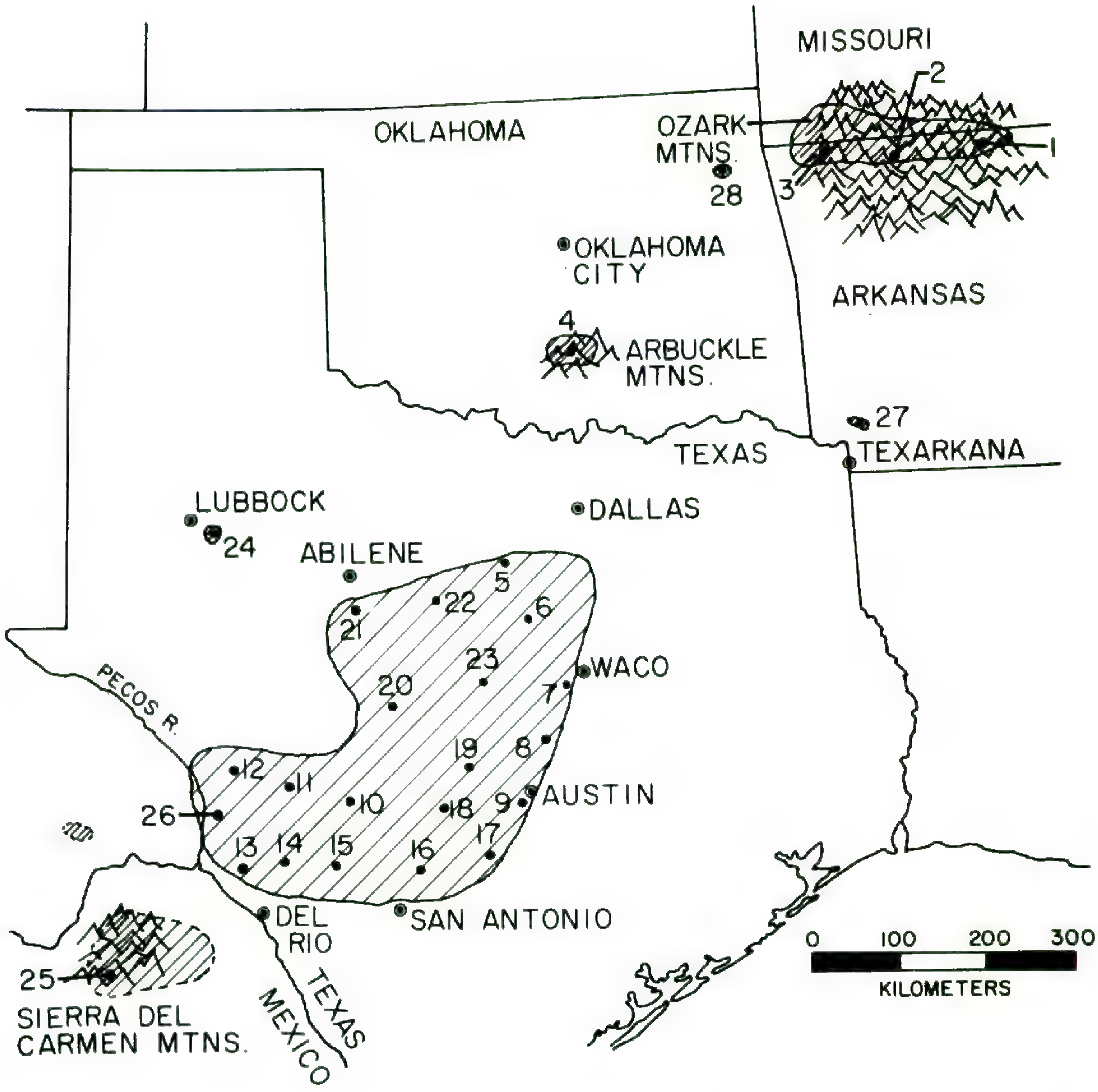


FIGURE 1. Distribution of *Juniperus ashei* showing the 28 populations sampled for this study. The exact distribution of *J. ashei* in northern Mexico is not known and is indicated generally by a dashed line.

be an excellent taxon to test some of the hypotheses advanced by Ehrlich & Raven (1969) in regard to gene flow versus selection in the maintenance of species.

Previous research (Adams & Turner, 1970; Adams, 1975a) has shown that the terpenoids of this taxon exhibit a remarkably high similarity between central Texas and the Ozarks (Fig. 2). However, many significant differences were found between populations 12, 13, and 17 and the other populations. One tree of *J. ashei* (number 116 in Fig. 2) was discovered in Mexico and found to cluster with the atypical populations (12, 13, 17). This, along with similar evidence in *J. pinchotti* populations (Adams, 1975b) seemed to imply that relicit migrations have been very important in the establishment of these patterns.

Evidence from rat middens and palynology in the southwestern United States is considerable (King, 1973; Mehringer et al., 1970; Van Devender & King, 1971; Wells, 1965, 1966, 1970; Wells & Berger, 1967; Whitehead, 1972; Wright, 1970)

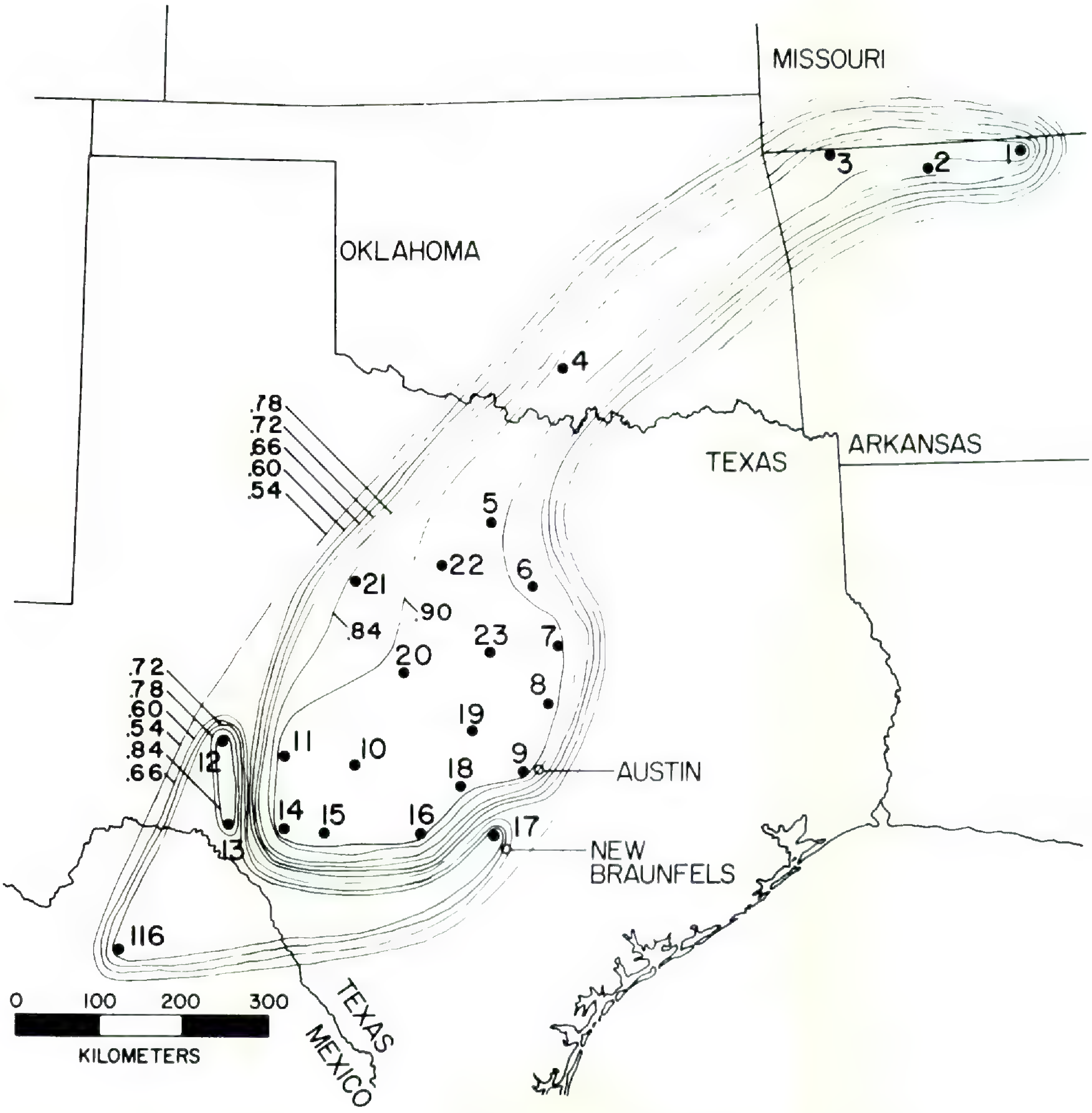


FIGURE 2. Contoured similarities based on 54 terpenoid characters, F-1 weighted. Notice the uniformity from central Texas to the Ozarks and the clustering of populations 12, 13 and 17 with tree 116 from northern Mexico (from Adams, 1975a).

that the Pleistocene ice advances pushed boreal and temperate species to lower elevations and southward. The northern Chihuahuan desert was certainly invaded by *Juniperus* (Wells, 1966) and crossed repeatedly. Even so, the data presented by Adams (1975a) for the close similarities of populations 12, 13 and 17 to northern Mexico *J. ashei* have remained somewhat tentative. This is due to the use of only 1 tree (number 116) from northern Mexico and the fact that no morphological data were used except in the largely preliminary study by Adams & Turner (1970).

In this study I will remedy these shortcomings by reporting on 15 trees of *J. ashei* from northern Mexico (population 25 in Fig. 1), as well as 4 additional populations: Post (near Lubbock), 24; Pandale, 26; Texarkana, 27; Saline Creek, Oklahoma, 28 (see Fig. 1). In addition, I report data on 16 morphological

Table 1. Sixteen morphological characters and states scored for 15 trees from each of the 28 populations of *J. ashei* sampled (Fig. 1). Missing data was coded by a –1.0 for a flag in statistical analysis.

Character	States (if applicable)
FDI	FEMALE CONE DIAMETER: avg. of up to 10 and not less than 4 (in mm).
FCO	FEMALE CONE COLOR: 1.0–4.0 (blue-yellow/brown).
SPF	SEEDS PER FEMALE CONE: avg. of up to 10 cones scored, not less than 4.
BLM	BLOOM ON CONE: 1.0–3.0 (none to very heavy coating).
SEA	SEED AREA: seed length × width, avg. of 10 seeds and not less than 4.
SER	SEED WIDTH/LENGTH: avg. of 10 seeds and not less than 4.
WGA	WHIP LEAF GLAND AREA: whip leaf gland width × length; avg. of 5 glands.
WGR	WHIP LEAF GLAND LENGTH/WIDTH: ratio, avg. of 5 glands.
WLM	WHIP LEAF MARGINS: 1.0–4.0 (smooth-heavy serration) avg. of 5 leaves.
WGP	WHIP GLANDS/PROTRUSION: 1.0–3.0 (sunken-smooth-protrudes), avg. of 5 glands.
WRP	WHIP GLANDS RUPTURED: 1.0–3.0 (none-some-almost all), avg. of 5 observations.
B/S	WHIP LEAF BLADE LENGTH/SHEATH LENGTH: avg. of 5 leaves.
G/S	WHIP LEAF GLAND LENGTH/SHEATH LENGTH: avg. of 5 leaves.
SLL	SCALE LEAF LENGTH: avg. of 5 leaves.
L/B	SCALE LEAF LENGTH/BRANCH WIDTH: Ratio of scale leaf length to the width of the branch (twig) where that scale leaf was borne. Avg. of 5 measurements.
BAN	BRANCHING ANGLE: Angle of branching of ultimate twig, avg. of 5 measurements (each to nearest 5 degrees).

characters, as well as peroxidases, from leaves. Finally, I compare these 3 sets of characters both in regard to their use in the analysis of populational differentiation and in the analysis of variability within populations.

Materials and Methods

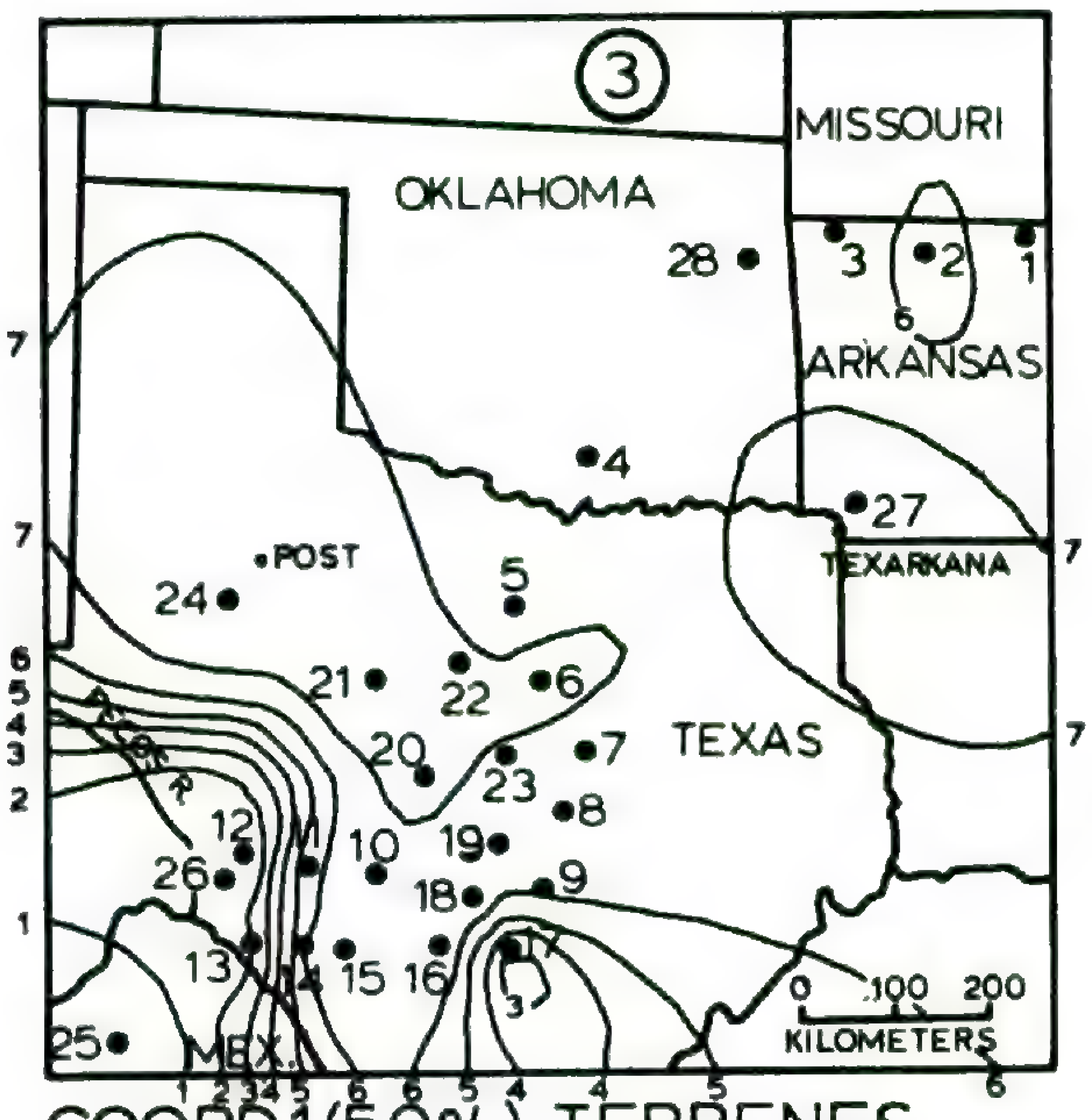
Twenty-eight populations of *J. ashei* were sampled throughout the natural range (Fig. 1). For the terpenoid and morphological characters, 15 trees were sampled from populations 1 through 23 in December, 1970, and 15 trees were sampled from populations 24 through 28 in December and January, 1974–1975, to complete the sampling. The sampling methods are given in Adams & Turner (1970), except that in 1974–1975, the foliage was generally frozen within a few hours in the freezer of our field trailer. Voucher specimens are on file at Colorado State University. All samples from each of the two sampling periods were placed in a random sequence for distillation as advocated by Adams (1975c). These procedures convert the temporal changes in foliage, oils, columns, etc. to random variables. Therefore population differentiation patterns can be readily separated from experimental procedural errors in the statistical analysis phase. The volatile terpenoids were steam distilled for 2 h as outlined by Adams (1970) and the extracts were kept at –20°C until analyzed by gas/liquid chromatography. Separation was made on a 200 ft × 0.02 in. capillary column (wall coated with PEG 20M) as described by Adams (1975a). The identities of the terpenoids of *J. ashei* are given in von Rudloff (1968) and Adams & Turner (1970). Individual peaks were quantified with an electronic digital integrator and automatically punched onto computer cards.

Sixteen morphological characters were scored as outlined in Table 1 for 15 specimens of 28 populations. Some fruit (female cones) and seed characters were not scored (and were thus set to –1.0 as a flag) since not all trees sampled had female cones.

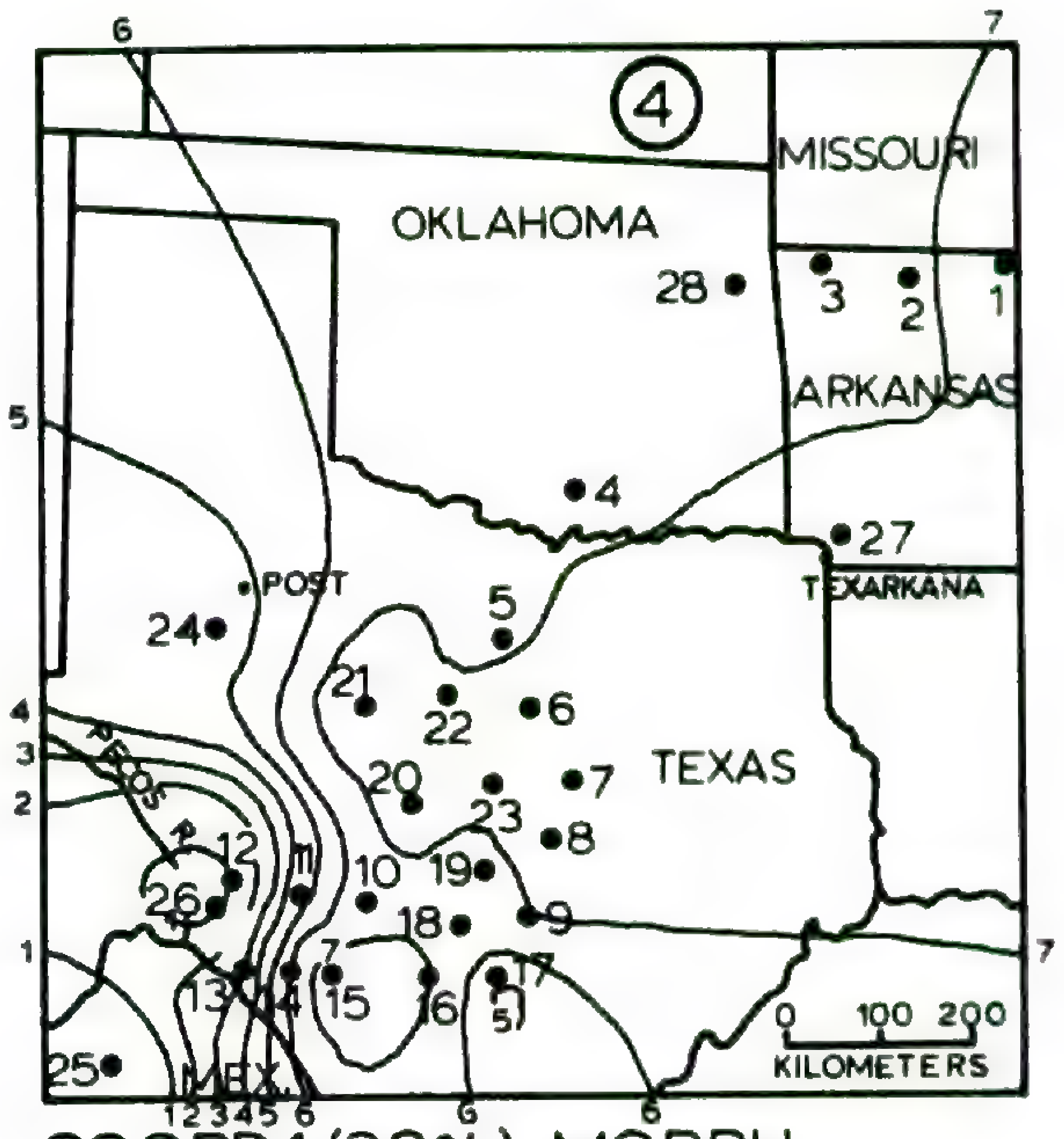
One hundred and forty-two terpenoids were subjected to analysis of variance (ANOVA) to determine which characters showed significant differences among populations. Fifty-nine terpenoids had F ratios greater than 1.0, a maximum population average greater than 0.1% and were used to compute F-1 weighted (Adams, 1975c) mean character differences (MCD or Manhattan metric) similarity measures between populations (see Adams, 1972, for exact formulation). This similarity matrix (28×28) was then used as input for principal coordinate analysis (Gower, 1966, 1967; Williams et al., 1971) to factor the similarity matrix into major coordinates of variation. The first 3 principal coordinates were used to contour map populations as they were ordinated on each of the orthogonal axes.

The 16 morphological characters were also analyzed by ANOVA and the Student-Newman-Keuls (SNK) multiple range test was applied ($P = 0.05$) to determine which populations were significantly different. Fifteen morphological characters (FEMALE CONE COLOR was omitted, $F = 0.88$) were used to compute a similarity matrix which was then factored by principal coordinates. The first 3 coordinates were contour mapped as outlined above.

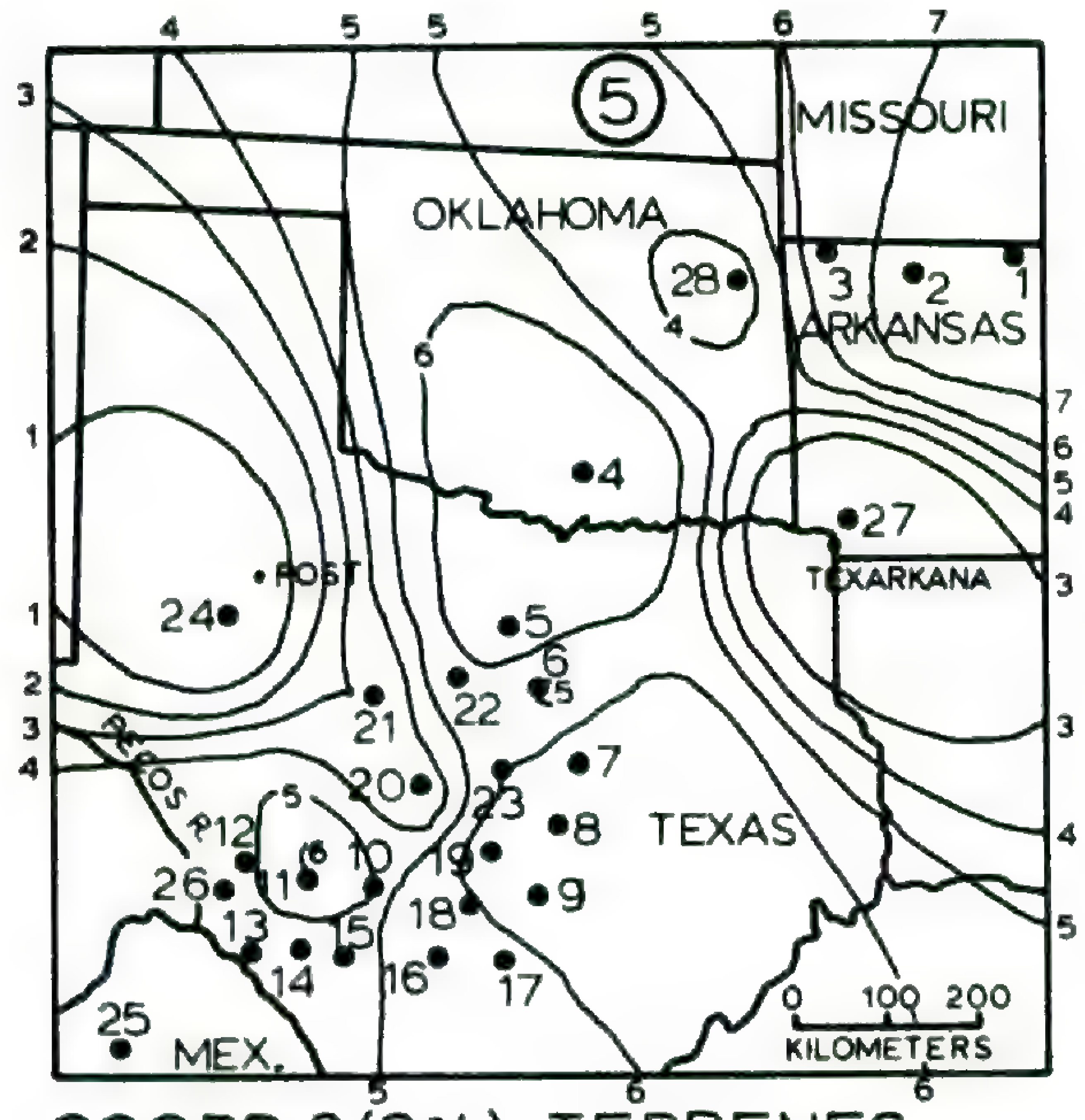
For the peroxidase work, foliage of 30 plants (occasionally less, see Kelley, 1976) were sampled from 15 populations in November–December, 1974, and frozen in the field trailer within a few hours. This foliage was kept frozen until extracted. The enzymes were extracted by grinding the foliage in liquid nitrogen with alumina then adding an extraction buffer of 0.10 M trismaleate, pH 7.00 containing: 0.02 M sodium tetraborate; 0.25 M sodium ascorbate; 0.02 M sodium meta-bisulfite; 0.02 M sodium diethldithiocarbamate (DIECA); 0.01 M germanium dioxide; 10% (v/v) dimethyl sulfoxide (DMSO) plus polyvinylpolypyrrolidone (PVPP), 10 gms/50 ml buffer. The complete instructions are lengthy and the interested reader is referred to Kelley (1976) and Kelley & Adams (1977a) for complete details. The peroxidases were concentrated and electrophoresed on acrylamide gels (discontinuous 4.5, 6, and 8% anodic, see Kelley, 1976) within 72 hours from the time of extraction. Although Kelley (1976) analyzed peroxidases, esterases, and an alcohol dehydrogenase, I am only using the peroxidase data since it showed much of the same pattern of variability as the other systems (Kelley, 1976). Peroxidases in *Juniperus* are little effected by seasonal differences (Kelley & Adams 1977a), and peroxidases are generally very stable (Kelley, 1976). Peroxidases were stained with o-tolidine/H_2O_2 (Denna & Alexander, 1975). An aggregate total of 23 peroxidase bands were found in the 15 populations of *J. ashei* sampled. In cases where bands were very close together on the gel, samples were corun to determine which electromorphs were different. These bands were each scored as 1.0 (present) or 0.0 (absent) for each plant and then subjected to ANOVA to obtain some estimate of F ratios for character weighting. Of course, ANOVA of qualitative data has a tendency to underestimate the F ratios, but this did provide a crude method to obtain relative character weights. Sixteen peroxidases had F greater than 1.0 and were



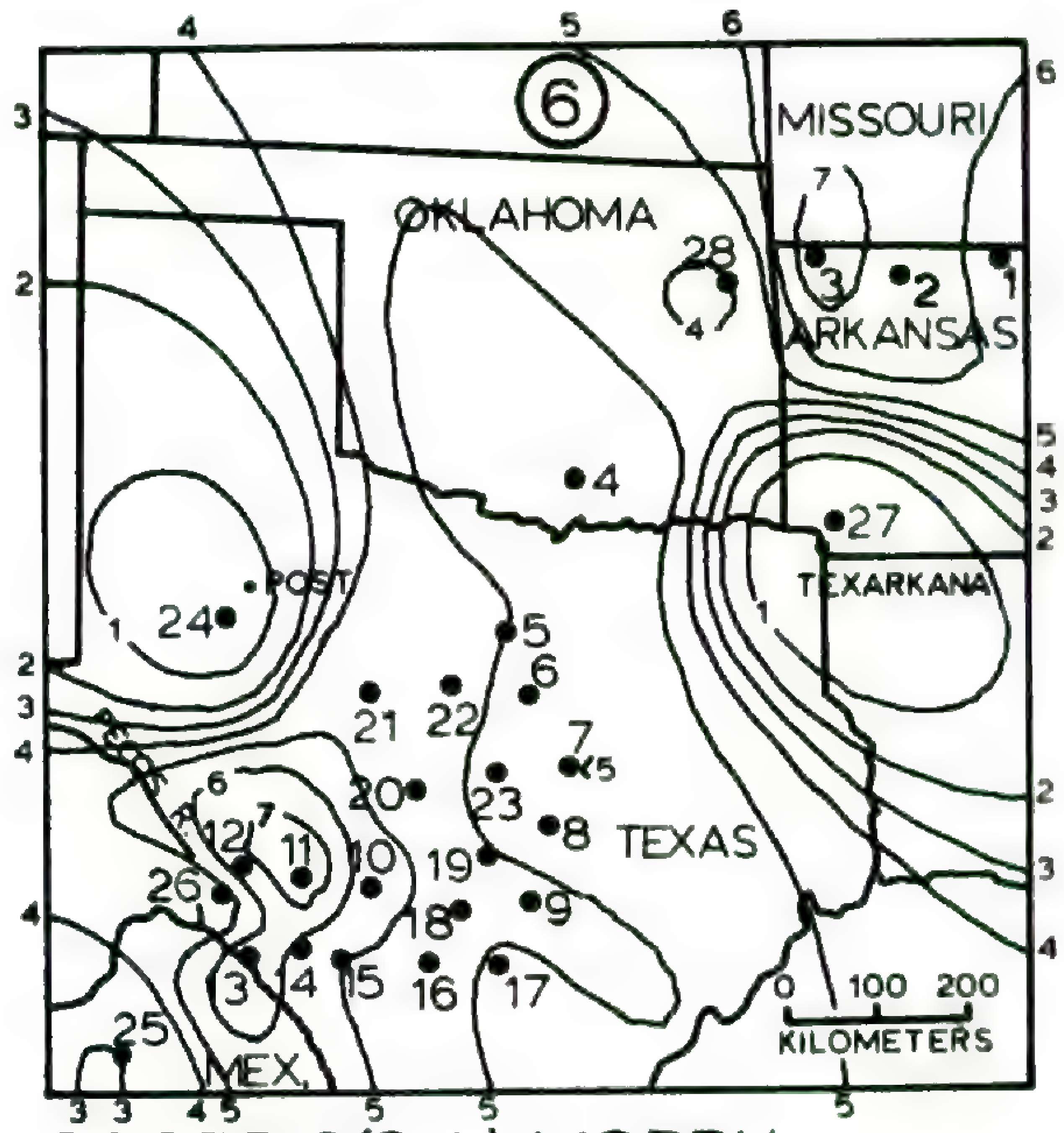
COORD.1(50%), TERPENES



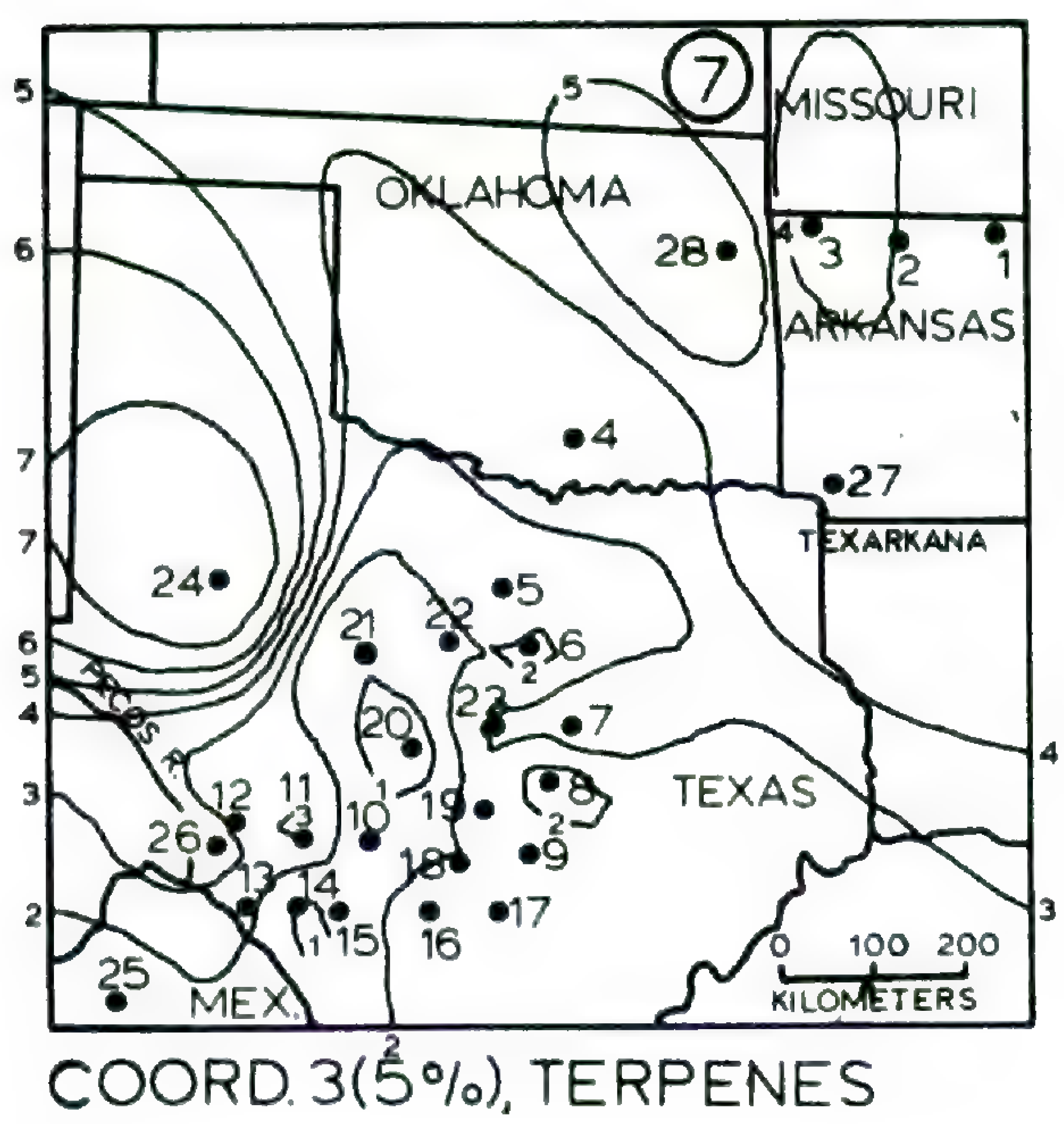
COORD.1 (38%), MORPH.



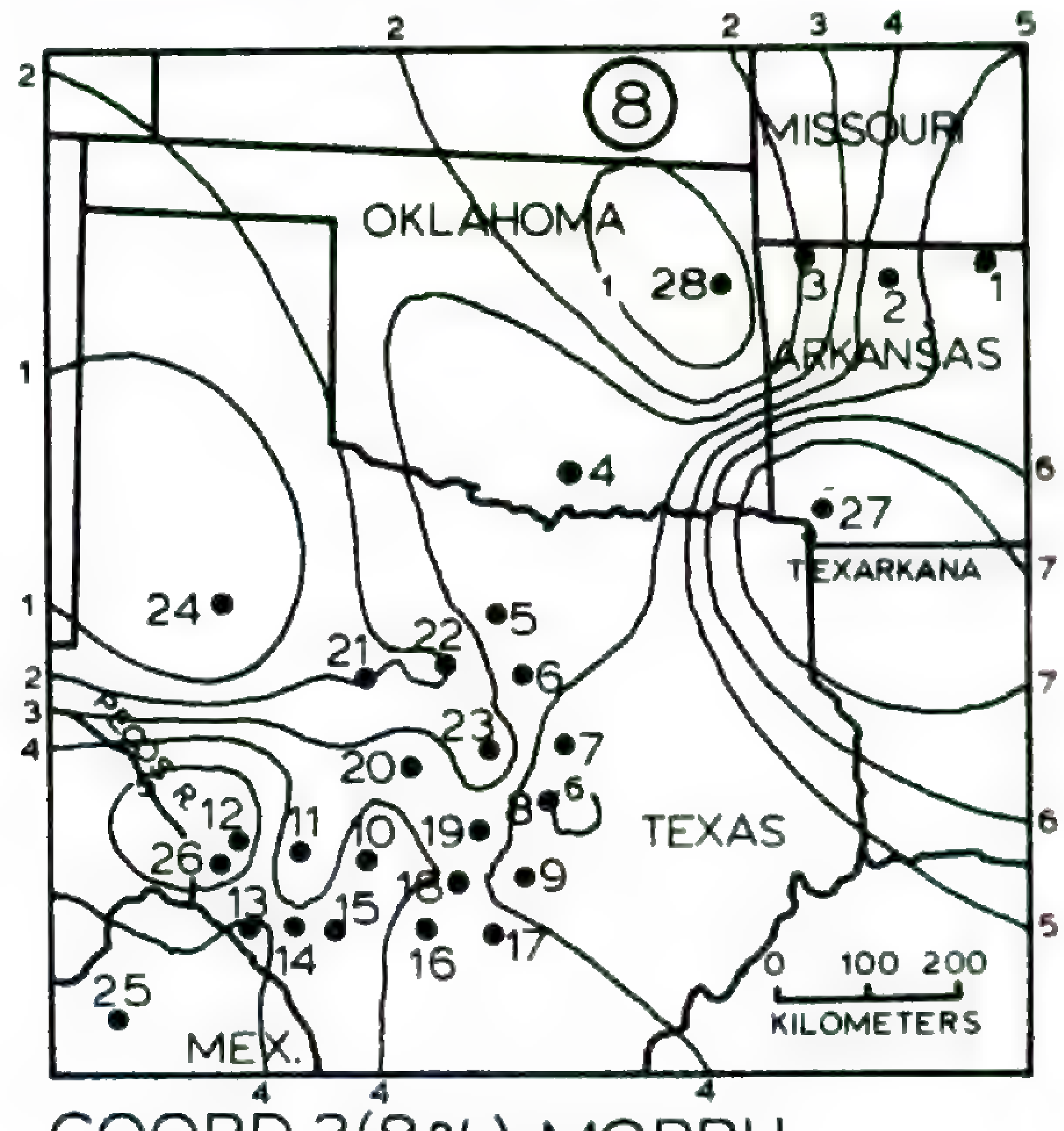
COORD. 2 (9%), TERPENES



COORD. 2(9%), MORPH.



COORD. 3(5%), TERPENES



COORD. 3(8%), MORPH.

not uniformly unique to one population. Similarity measures were computed as outlined above, and the similarity matrix (15 × 15) was factored to obtain principal coordinates. The first 2 coordinates were contour mapped for comparison of regional trends.

For the analysis of within populational variability, 3 sets of similarity measures were calculated using all terpenoid, morphological, and peroxidase characters, equally weighted. It appears that F weighting is not desirable when examining intrapopulational variation. These analyses resulted in 3 kinds of similarity matrices (terpenoid, morphological, and peroxidase) for each population. The average similarity ($\overline{Sr}$) was then computed for each population along with the coefficient of phenetic variation ($CPV = Sd_{\overline{Sr}}/\overline{Sr}$). The $\overline{Sr}$'s and CPVs were then contour mapped to examine regional trends of intrapopulational variation.

Populational Differentiation

The principal trend in the terpenoid similarities is that of the differentiation of populations 25, 26, 12, 13 and 17 from the rest of the populations (Fig. 3). From these coordinate loadings one can see (Table 2) that 50% of the variation in the similarities is mostly due to the divergent nature of populations 25, 26, 12, 13 and 17. The high negative loading of population 17 onto coordinate one indicates that population 17 (New Braunfels, Texas) has considerable affinities with the west Texas and Mexico plants. It is interesting to compare the major trend of the terpenoids with that of the morphology (Fig. 3 vs. Fig. 4). This major trend in the morphology accounts for 38% of the variation in similarities and is practically identical to the major trend of the terpenoids. A couple of exceptions are that the Post population (24) seems more similar to the west Texas-Mexico populations in the morphology, while the New Braunfels population (17) is not quite as different from the central Texas populations in its morphology as in its terpenoids. In both cases, from central Texas to the Ozarks a picture of uniformity is presented. It might be noted that this compares very closely with the contoured terpenoid phenogram in Fig. 2 (from Adams, 1975a). It appears that the major coordinate of principal coordinates analysis is the dominant

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FIGURES 3–8.—3–4. Contoured loadings of principal coordinate 1 extracted from similarity measures among populations, (see Tables 2–3).—3. This pattern extracted 50% of the variation from the terpenoid similarity matrix. Notice that this pattern is the principal pattern previously shown (Fig. 2). Contours: 1 = –0.70; 7 = 0.18.—4. This pattern accounted for 38% of the variation from the morphological similarity matrix. The Post population (24) shares some affinities to the west Texas-Mexico populations. Population 17 seems a little less divergent in its morphology than its terpenoids (Fig. 3). Contours: 1 = –0.64; 7 = 0.13.—5–6. Contoured principal coordinate 2.—5. This trend (9%, terpenoids) seems to be due to the divergence of populations 24, 27, and 28, plus sampling differences (see text). Contours: 1 = –0.37; 7 = 0.16.—6. This trend (9%, morphological) seems to be due to procedural differences in scoring the morphological characters (see text). Contours: 1 = –0.32; 7 = 0.16.—7–8. Contoured principal coordinate 3.—7. Divergence of the Post (24) population is most evident along this coordinate (5%, terpenoids). Contours: 1 = –0.27; 7 = 0.28.—8. Note the strong divergence between populations 27 and 28 (8%, morphological). Contours: 1 = –0.22; 7 = 0.27.

TABLE 2. Principal coordinate analysis of similarity matrices using terpenoids, morphology, and peroxidase characters for the computations of similarity measures between populations of *J. ashei*. All eigenroots were extracted from each matrix until they failed to converge. It is thought that when eigenroots begin to level off in values, additional roots represent only random error variance.

TERPENOIDS (Srs based on 59 terpenoids, 28 × 28 matrix) 71% of variation extracted by 5 roots.										
Eigenroots	3.56	0.66	0.36	0.29	0.25					
% variation extracted	49.6	9.2	5.1	4.0	3.6					
MORPHOLOGY (Srs based on 15 morphological characters, 28 × 28 matrix) 72% of variation removed by 7 roots.										
Eigenroots	2.40	0.64	0.53	0.36	0.34	0.30	0.26			
% variation extracted	35.9	9.5	8.0	5.4	5.1	4.6	3.9			
PEROXIDASES (Srs based on 16 peroxidases, 15 × 15 matrix) 93% of variation extracted by 10 roots.										
Eigenroots	1.68	0.85	0.62	0.53	0.35	0.30	0.27	0.21	0.19	0.18
% variation extracted	30.1	15.2	11.2	9.5	6.3	5.4	4.8	3.8	3.5	3.2

theme of a single linkage phenogram (see Adams, 1975a). Thus, we see that the west Texas-Mexico type populations account for 50% and 38% of the variation in the terpenoid and morphological similarities, respectively.

The second coordinate extracted from the terpenoid similarity matrix largely separates the small island populations at Post (24), Texarkana (27), and Saline Creek (28) from the rest of *J. ashei* (Fig. 5). These populations, along with 25 and 26, were collected and analyzed 4 years later (1974) than the other populations (1970 collections). Therefore part of these differences may be due to sampling methods, seasonal variations, and different gas chromatographic conditions. However, populations 25 and 26 seem to cluster well with populations sampled in 1970, so this factor may be only a minor cause of this trend. It seems that this small amount of variation (9%) is chiefly accounted for by the divergence of these 3 small, isolated populations (24, 27, 28), along with a contribution resulting from different sampling and analysis times. The second coordinate of the morphological similarity matrix (Fig. 6) is clearly due to the fact that populations 24, 26, 26, 27, and 28 were sampled and analyzed in 1974 rather than with the other populations (sampled and analyzed in 1970). It is felt that most of these differences (approximately 9% of the variation in the similarity matrix) are due to the fact that a different technician measured the morphological characters of populations 24, 25, 26, 27, and 28 (1975) than the other populations (1970–1972). Even with close supervision and training, it is very difficult to get two people to score morphological characters in the same manner. My experience has been that comparisons between morphological data sets scored by completely different research projects is almost impossible. If we consider that the eigenroots of about 5% may be mostly random noise (see below), then the 9% of coordinate 2 is only about twice the experimental error but 25% the size of the major trend.

The third coordinate does not appear to be very significant in the terpenoid

similarity matrix since only 5.1% of the variation was extracted and the eigenroots have leveled off at this value (Table 2). Contouring of this coordinate (Fig. 7) shows that most of the variation along this axis is due to population 24 at Post. This population is on one of the most unusual sites that I have seen for *J. ashei*. It is in a deep ravine, cut into the Permian red clay, just east of the Llano Estacado. The stand is occasionally mixed with *J. pinchotii*, with *J. ashei* found in the more mesic spots. This trend could represent a response to microhabitat selection or environmentally induced plasticity. Transplant studies will probably be needed to answer this question. Another trend is that the northern-most (including Post) populations seem to be more heavily loaded onto this coordinate than those populations in the central and southwestern portion of the range.

The third coordinate of the morphological similarity matrix extracted 8.0% of the variation and might be significant as the 4th through 7th roots seem to have asymptoted to about 4 or 5%. The contour map of this coordinate (Fig. 8) shows a northwest-southeast trend across the populations, somewhat like that in Fig. 7, except there is a decided split between the Texarkana population (27) and those to the north and west. This population (27) is almost as atypical for *J. ashei* as the one at Post, Texas (24). At population 27, *J. ashei* is found on a small (few acres?) limestone outcrop that is gently sloping and very moist (1,143–1,270 mm of precipitation per year). It is a mixed stand with some *J. virginiana*. Whether this pattern represents some small microhabitat selections or environmentally induced plasticity in the morphology must await transplant studies for additional information.

In any case, it is obvious that the major trend in both the terpenoids and morphology is the differentiation of populations 25, 26, 13, 12, and 17 from the rest of the species.

Principal coordinate analysis of the similarity matrix based on peroxidases (Tables 2–3) yielded quite different results. A most notable difference being that 10 eigenroots were extracted from a 15 × 15 matrix, whereas only 5 and 7 roots accounted for most of the definable variation in the much larger (28 × 28) matrices of the terpenoids and morphology. This seems to indicate that the peroxidases are varying in many different directions, whereas the terpenoids and morphology seem to display much more directional or concurrent variation. Another interesting facet is that the eigenroots of the terpenoid and morphological similarity matrices quickly decreased to rather constant values after 2 and 3 roots, whereas the roots of the peroxidases seem to tail out much farther. This seems to imply a considerable amount of independence among the peroxidases. Examination of the first coordinate of the peroxidase similarity matrix (Fig. 9) reveals a northeast-southwest pattern (remember that only the 15 populations marked with an asterisk were analyzed for peroxidases). The Texarkana (27) and Junction (10) populations are most similar to each other, and the Ozark populations (1, 2) are most similar to the north Texas (5, 7) and west Texas-Mexico populations (12, 25). This trend is unlike any other seen in either the morphological or terpenoid data. The divergence of the Texarkana population (27) from the Ozark (1, 2) and north Texas (5, 7) populations would be easy to explain (if one ignores the morphological and terpenoid data) as genetic drift and/or

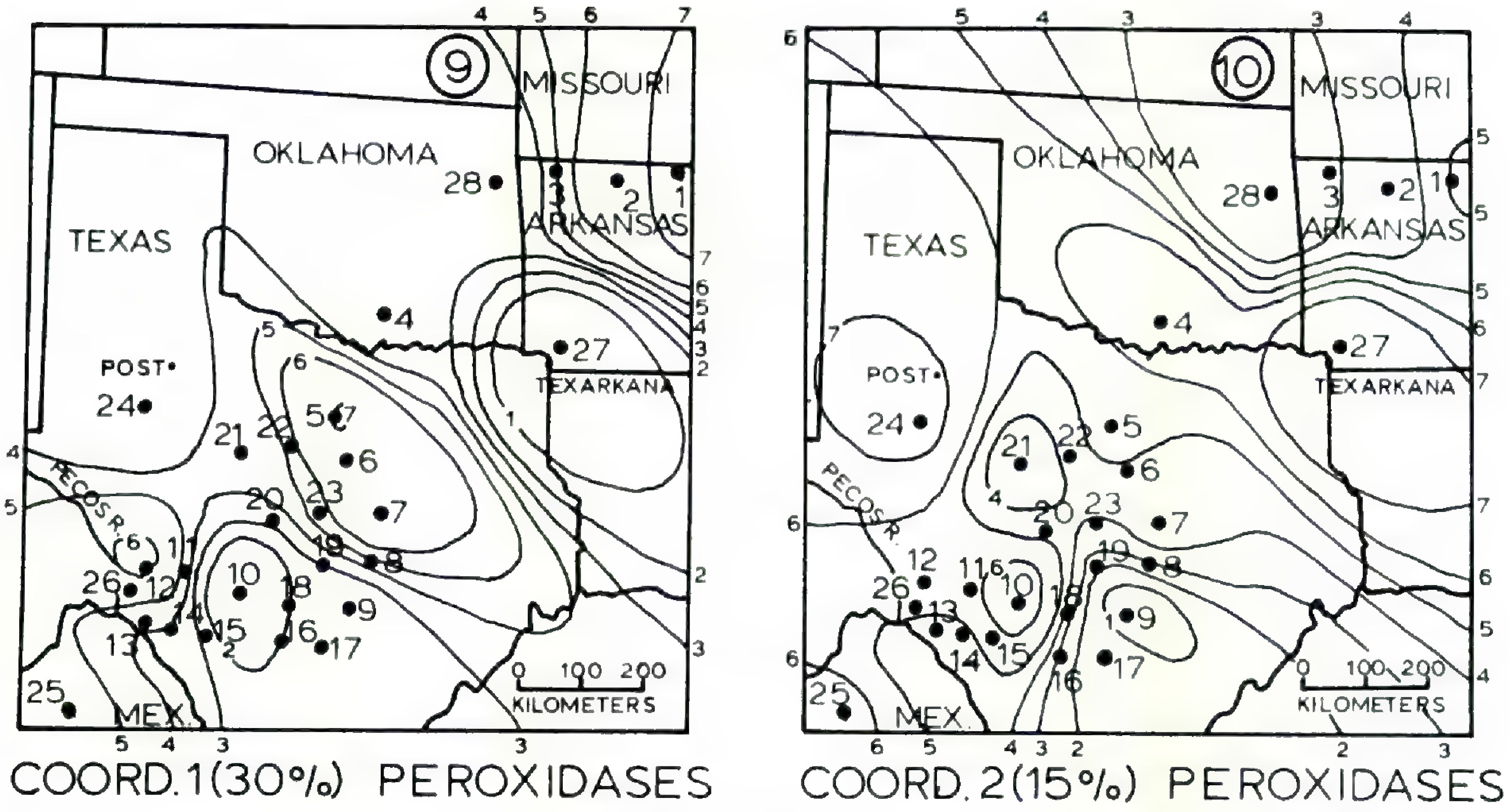
TABLE 3. Coordinate loadings (principal coordinates 1, 2, 3 in each case) for populations onto coordinates. These coordinate loadings were used for generating the contour maps in successive figures. Note the close correspondence between coordinate 1 for the terpenoids and morphology. Values in parenthesis indicate the amount of the variation in the Sr matrix accounted for by each of the coordinates.

	Terpenoids			Morphology			Peroxidases		
Population	C_1 (50%)	C_2 (9%)	C_3 (5%)	C_1 (38%)	C_2 (9%)	C_3 (8%)	C_1 (30%)	C_2 (15%)	C_3 (11%)
1	0.11	0.18	0.13	0.16	0.06	0.15	0.52	0.06	0.11
2	-0.02	0.20	0.08	0.13	0.13	0.10	0.32	-0.17	0.04
3	0.17	0.12	0.03	0.06	0.21	-0.15	—	—	—
4	0.15	0.11	0.04	0.13	0.06	-0.02	-0.16	0.21	-0.14
5	0.13	0.17	0.02	0.12	0.00	0.00	0.44	0.06	0.12
6	0.23	-0.08	-0.09	0.18	0.09	0.01	—	—	—
7	0.13	0.18	0.10	0.20	-0.02	0.11	0.38	-0.04	0.02
8	0.15	0.04	-0.14	0.20	0.09	0.15	—	—	—
9	0.11	0.18	0.01	0.17	-0.05	0.11	-0.27	-0.51	-0.05
10	0.21	-0.04	-0.14	0.13	0.03	0.10	-0.50	0.20	-0.20
11	0.11	0.15	0.06	-0.14	0.27	-0.14	—	—	—
12	-0.84	-0.05	-0.03	-0.71	0.28	0.20	0.31	0.16	-0.04
13	-0.78	-0.03	-0.03	-0.49	0.18	-0.02	-0.06	-0.06	0.04
14	0.21	-0.14	-0.20	0.20	0.06	0.04	—	—	—
15	0.20	-0.05	-0.10	0.26	-0.04	0.10	—	—	—
16	0.18	0.06	0.02	0.18	-0.05	-0.04	—	—	—
17	-0.67	0.02	-0.00	0.23	0.05	-0.06	-0.33	-0.34	0.10
18	0.18	0.03	-0.08	0.14	-0.05	0.05	—	—	—
19	0.10	0.16	-0.03	0.09	0.00	-0.07	—	—	—
20	0.22	-0.23	-0.18	0.17	-0.05	0.03	—	—	—
21	0.26	-0.21	-0.13	0.17	0.01	-0.15	-0.02	-0.11	-0.28
22	0.19	0.07	-0.07	0.13	-0.07	-0.18	—	—	—
23	0.18	0.08	0.07	0.14	0.03	-0.17	—	—	—
24	0.22	-0.42	0.32	-0.14	-0.34	-0.27	-0.11	0.30	-0.42
25	-0.78	-0.07	-0.07	-0.71	-0.16	-0.06	0.18	0.17	0.15
26	-0.71	-0.05	0.08	-0.72	-0.26	0.13	—	—	—
27	0.20	-0.26	0.11	0.16	-0.36	0.31	-0.58	0.34	0.49
28	0.16	-0.13	0.19	0.02	-0.09	-0.26	-0.14	-0.28	0.07

founder's effect, but the peroxidase similarity to the Junction population (10) rather stretches the point.

Coordinate two of the peroxidase similarity matrix shows (Fig. 10) high loadings of populations 27, 4, 24, 10, and 25. This coordinate seems to be a random assortment of populations distributed across the range of *J. ashei*. Similar variation (high similarities across disjunct populations and a random mosaic pattern) has been previously observed in nonsignificant variation of individual morphological characters (see Adams & Turner, 1970, for several contoured morphological characters). Coordinate three shows another pattern of mosaic variation and the interested reader is referred to Kelley & Adams (1977b) for more detailed maps of peroxidases, esterases, and alcohol dehydrogenases.

How can we interpret these conflicting results? One way to view geographical variation is to consider the number of gene differences needed to produce the observed changes. For morphological characters, Charles & Goodwin (1943) have shown that in *Solidago* many morphological characters used in taxonomy



FIGURES 9–10.—9. Contoured loadings of principal coordinate 1, extracted from the F-1 weighted peroxidase similarity measures among populations (see Tables 2–3). This coordinate extracted 30% of the variation from the matrix. Only those 15 populations marked with an asterisk were analyzed for the peroxidases. See text for discussion. Contours: 1 = −0.51; 7 = 0.43.—10. Contoured principal coordinate 2 (15% of the variation, peroxidase similarities). No regional trends were uncovered in this or any of the successive coordinates extracted. See text for discussion. Contours: 1 = 0.42; 7 = 0.28.

are controlled by a minimum of 4, 5, and 6 genes. Irving & Adams (1973) in a study of *Hedeoma* terpenoids found that those terpenoids were controlled by a minimum of 1, 2, and 3, but up to 7, genes which agrees with the work on *Pinus* by Hanover (1966) and others. The peroxidase electromorphs isolated on gels represent probably no *more* than 1 gene for each 2 bands in the composite. Suppose we assume that the 15 morphological characters are each controlled on the average by 5 genes, the 59 terpenoid characters each are controlled by 2 genes (average), and the 16 peroxidase bands are each controlled by 1 independent allele, with 2 alleles (simple codominance) per gene. This means that the pattern displayed by the morphological data sampled a *minimum* of 75 genes, with a *minimum* sample of 118 genes for the terpenoids, and a *maximum* sample of 8 genes for the peroxidases. Of course, we have ignored pleiotropy, epistatis, and linkage, but we have no *a priori* knowledge that these factors are of differential genetic importance in any of these 3 kinds of data. To obtain a random sample of the genome, one would have to favor the morphological and terpenoid data on the basis of sample size alone. Together the morphology and terpenoids (*minimum* of 193 genes) overshadow the peroxidase data (*maximum* of 8 genes). Even so it is striking that no logical regional trends emerged from the peroxidases (nor from the esterases or alcohol dehydrogenases, Kelley & Adams, 1977b). The problems of homology may account for much of this random similarity between widely, disjunct populations (e.g., population 10 and 27, Fig. 9). Homology between the morphology of these populations (Table 1) is practically assured. The terpenoid variation is almost totally quantitative in this taxon, and

the resolution obtained with capillary gas chromatography greatly increases the probability that peaks from different populations of a quantitatively varying species are in fact the same compound (although there is a small finite probability that different genes produce the same compound in different populations). On the other hand, the peroxidases were often found to be qualitatively varying between close, adjacent populations with a band being in very high frequencies in one population and totally missing from our sample in another population. The high similarities obtained in mosaic patterns (Figs. 9–10) are most readily explained by lack of homology between peroxidase bands, although parallel microselection could play an important role. As far as I know, there have been no cases showing that electrophoretic mobility, *per se*, is under selection (that is not to say that proteins bearing more positive or negative charges might not be selected due to substrate affinity, etc.).

Four hypotheses have been advanced (Adams & Turner, 1970) to explain the pattern of regional variation seen in the terpenoids and morphology of *J. ashei*. Two of these, sampling errors and parallel selection (in populations 17, 12, 13, 25, 26) have been pretty well disposed of by Adams (1975a). The other two, predominately southerly winds during pollination (December–January) and northward bird migration during the spring, and ancestral migration leaving relict populations, deserve additional discussion. The prevailing wind during the pollination period (December–January) is generally from the south on the Edwards Plateau (Arbingast et al., 1967). Thus, one might expect pollen to be generally blown northward. Coupled with the northward migration of Cedar waxwings and other birds that feed on *J. ashei* berries (female cones), this would tend to isolate population 17 from breeding with adjacent populations (9, 16, 18). This would also help explain the north-south line of differentiation between populations 12, 13 and 11, 14 (Figs. 3–4). Although these phenomena help explain the persistence of the pattern, they do little to explain the common patterns seen in populations 25, 26, 12, 13, and 17. Ancestral migrations leaving relict populations could help explain these patterns.

Pleistocene Patterns

Although there is considerable evidence of a continuous band of sclerophyllous vegetation from central Texas into northern Mexico during the Tertiary (Axelrod, 1975), I would like to focus on events of the Pleistocene, particularly the last pluvial and interglacial periods. I have reconstructed parts of the vegetation during the Wisconsin pluvial, 10,000–20,000 B.P., in Fig. 11. According to King (1973) the western Missouri Ozarks were covered with boreal spruce forest from about 25,000 to at least 13,000 B.P., with pine parkland preceding the boreal spruce. Since the pine parkland and boreal spruce forest both appear to have been pushed southward from the north (Dillon, 1956), I have assumed that the area south of the Ozarks may have been pine woodland or parkland (also see Bryant, 1969). A pine-spruce woodland seems likely in the Llano Estacado of northwest Texas (staked plains) according to Hafsten (1961). Bryant (1969) suggested that based on pollen profiles, the present Chihuahuan desert area around Del Rio, Texas (430 m) was a pinyon woodland. Wells (1966),

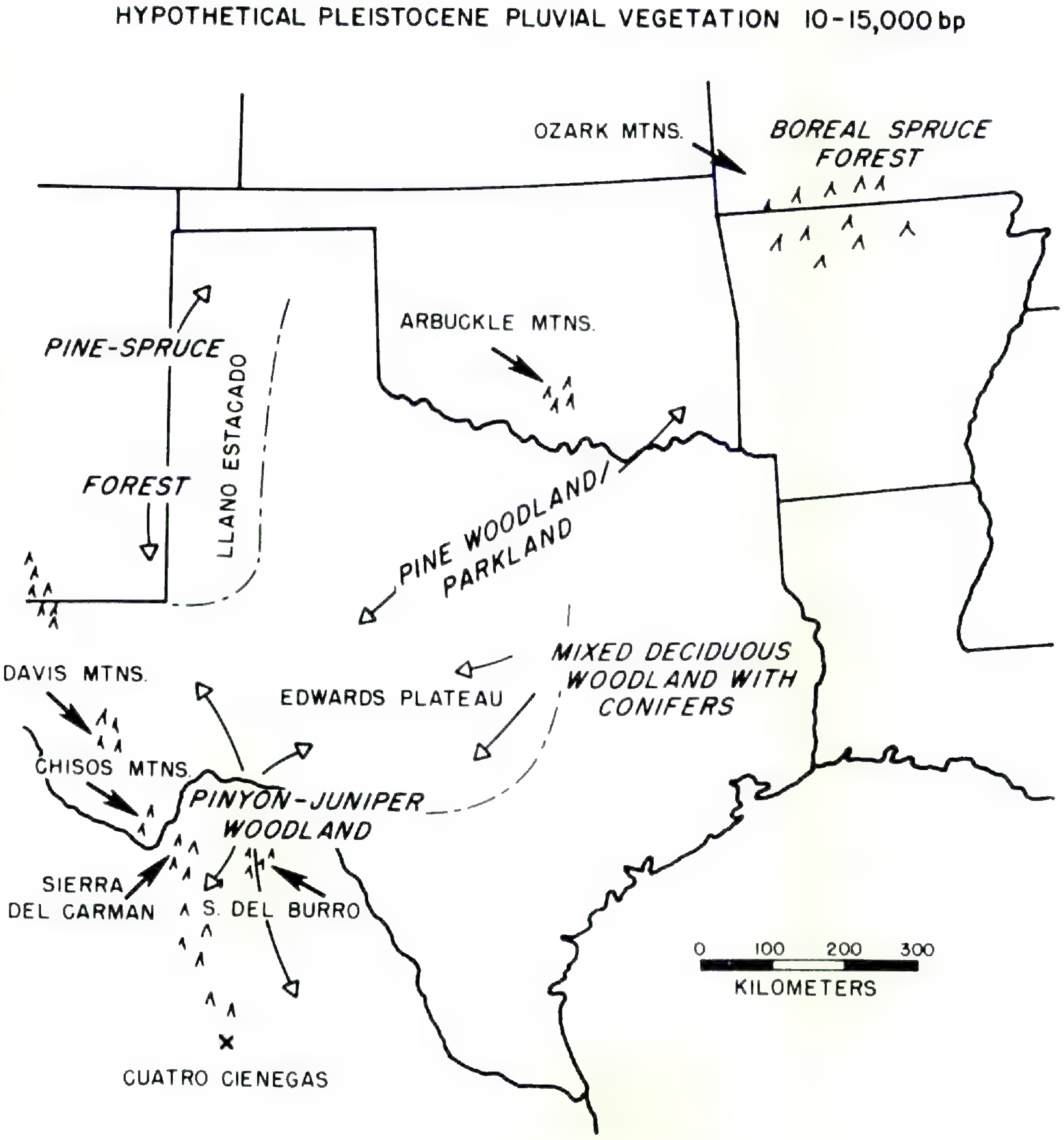


FIGURE 11. Hypothetical Pleistocene pluvial vegetation, 10,000–15,000 B.P. based on pollen profiles and rat midden data from the literature. See text for discussion.

using data obtained from rat middens from the Big Bend Texas region, concluded that the life zones descended about 800 m for pinyon-juniper (*J. pinchotii* in that case), allowing the advance of pinyon-juniper into most of the present desert region between Big Bend and Del Rio. Another important fact has been the recent discovery (D. H. Riskind, pers. comm.) of *J. ashei*, *J. pinchotii*, *J. flaccida*, and *J. scopulorum* from the Sierranas del Burro (Fig. 11). Since typical *J. pinchotii* has been found (Adams, 1975b) just south of the Sierra del Carman (growing with *J. ashei*), it appears that the Sierranas del Burro may have been an important refugium or island point in the pinyon-juniper woodland. A mixed deciduous woodland with conifers is postulated in central Texas (Bryant, 1969; based on a pollen profile).

TABLE 4. SNK tests for 15 morphological characters with F ratios greater than 1.0 in ANOVA. SNK tests were run at P = 0.05, $F_{0.05} = 1.58$, $F_{0.01} = 1.90$ (df = 27/380). Any two populations not underlined by a common line are significantly different. Populations are listed in decreasing order of their means from largest to smallest. Ranges refer to the maximum and minimum means over all populations for that character.

FEMALE CONE DIAMETER (FDI), F = 9.3, no obs. for populations 24, 27, range = (8.91–6.4 mm)

15 5 14 6 3 23 4 7 11 21 16 2 10 19 8 22 28 20 1 18 9 13 12 17 26 25

SEEDS PER FEMALE CONE (SPF), F = 9.7, no obs. for populations 24, 27, range = (1.69–1.01)

12 26 13 25 4 17 11 28 2 19 3 10 14 16 21 1 18 8 15 23 20 5 7 6 9 22

BLOOM ON FEMALE CONES (BLM), F = 1.2, no significant differences

SEED AREA (SEA), F = 9.8, no obs. for populations 24, 27, range (27.1–13.6 mm^2)

20 16 21 14 5 15 4 23 6 22 8 7 10 3 9 19 2 28 11 18 1 17 13 12 25 26

SEED WIDTH/LENGTH (SER), F = 1.3, no significant differences

WHIP GLAND AREA (WGA), F 9.2, range (0.93–0.31 mm^2)

12 25 11 13 3 26 23 17 5 6 28 14 7 20 16 21 4 18 1 22 24 15 19 10 8 2 9 27

WHIP LEAF GLAND LENGTH/WIDTH (WGR), F = 4.4, range (2.5–1.5)

13 25 17 26 5 12 11 4 1 19 8 2 7 14 3 27 22 16 18 20 6 9 10 23 15 28 24 21

WHIP LEAF MARGINS (WLM), F = 5.0, range (2.3–1.9)

24 28 25 22 23 26 16 13 21 27 5 17 9 6 19 18 20 14 4 3 15 10 7 1 12 8 11

WHIP LEAF GLANDS PROTRUSION (WGP), F = 2.6, range (3.00–2.87)

1 3 6 7 10 11 15 19 20 21 23 25 18 12 17 22 28 16 8 9 14 2 24 13 4 5 26 27

WHIP LEAF GLANDS RUPTURED (WRP), F = 2.7, range (1.08–1.00)

13 12 11 14 4 6 7 8 9 10 2 3 1 5 15 16 17 18 19 20 21 22 23 24 25 26 27 28

WHIP LEAF BLADE LENGTH/SHEATH LENGTH (B/S), F = 2.9, range (0.77–0.54)

24 25 2 26 9 12 11 1 27 28 14 15 16 10 6 5 13 19 22 20 21 4 7 3 8 18 23 17

WHIP LEAF GLAND LENGTH/SHEATH LENGTH (G/S), F = 16.7, range (0.41–0.22)

25 26 12 13 17 11 24 3 28 19 22 21 23 16 4 5 18 20 9 6 14 2 10 8 1 7 27 15

SCALE LEAF LENGTH (SLL), F = 4.1, range (1.74–1.43 mm)

28 27 24 25 19 7 18 16 1 22 15 26 14 21 20 4 5 23 11 13 9 17 12 3 2 8 6 10

SCALE LEAF LENGTH/BRANCH WIDTH (L/B), F = 4.1, range (1.43–1.15)

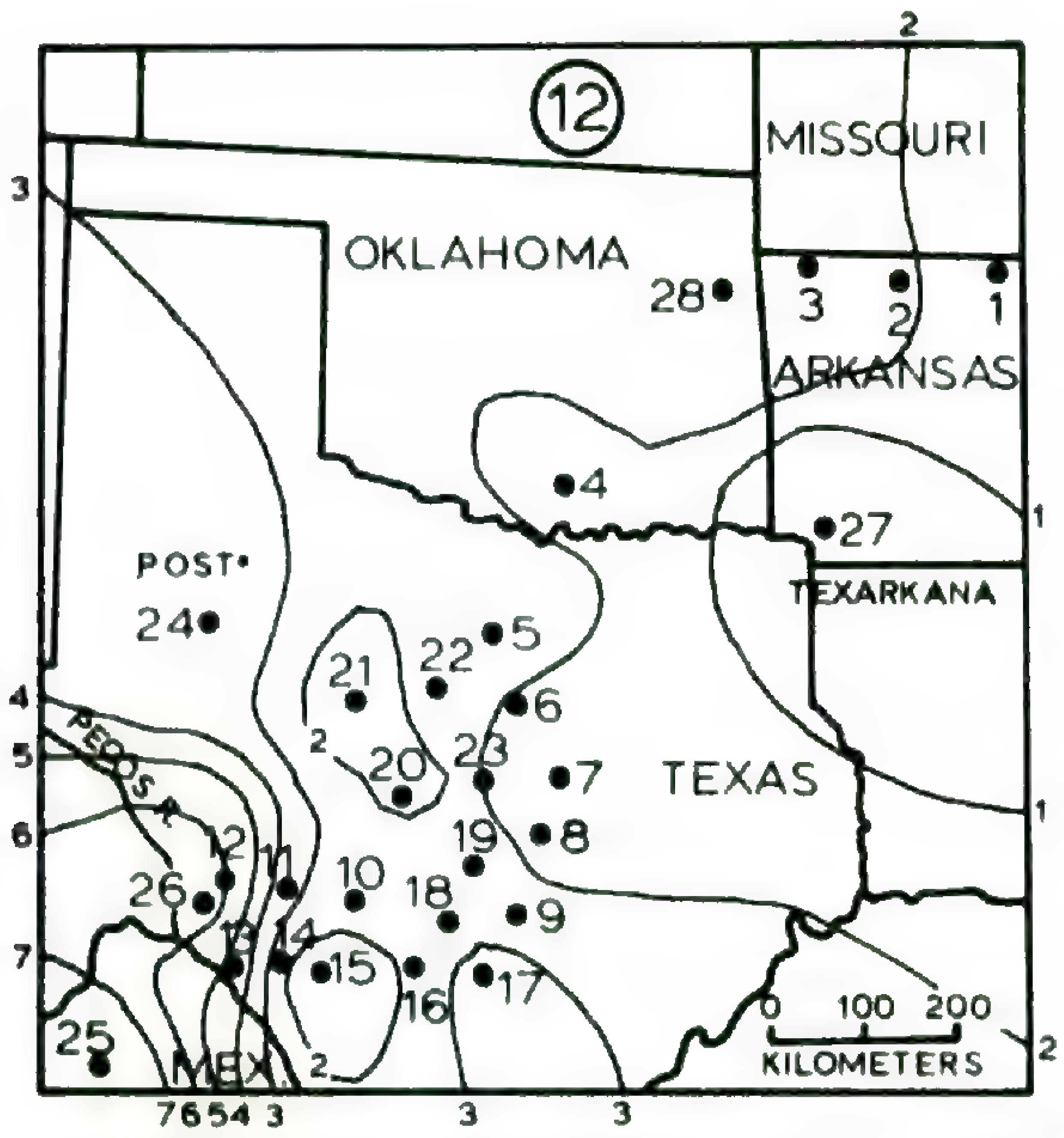
9 27 17 15 19 18 5 16 7 20 1 14 8 22 23 4 21 25 28 11 3 2 13 6 10 24 12 26

BRANCHING ANGLE (BAN), F = 9.5, range (55.2–39.9 degrees)

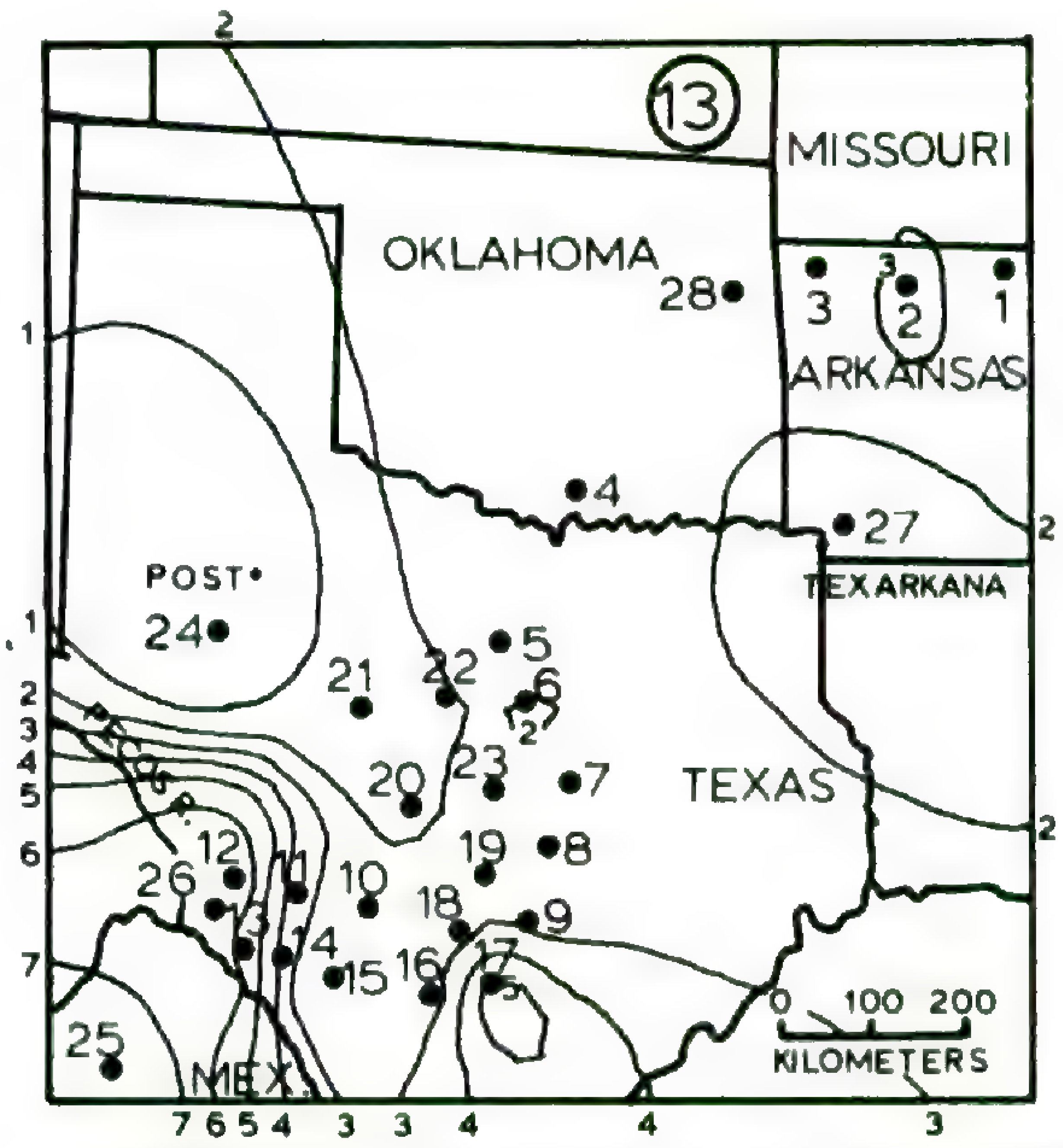
12 26 25 10 24 13 27 20 7 17 5 18 11 28 19 16 9 4 23 8 15 6 14 22 21 1 2 3

Life zones were pushed southward and compressed during the Wisconsin pluvial (Dillon, 1956), but how far they were extended into Mexico is not well known. Additional rat midden and pollen profiles are needed in northern Mexico and the Mexican plateau region. A study by Meyer (1973) in the Cuatro Cienegas basin (Fig. 11) revealed no changes in the pollen profiles during the past 30,000 years. He concluded that there was no evidence for pluvial nor hypsithermal (Deevey & Flint, 1957) periods at Cuatro Cienegas during the time sequence studied. This agrees with Dillon (1956: 174) who shows a considerable compression of life zones from Nebraska to south Texas but few differences past northern Mexico. It seems likely that any generalized Mexican refugium must have been in northern Mexico. One other point that seems relevant is that Wells (1966) mentioned that the pinyon found in the rat middens in the Big Bend area contained consistently 2-needled fasicles suggesting that the pine involved may not have been the predominately 3-needled *Pinus cembroides* Zucc, but perhaps *Pinus cembroides* var. *remota* E. L. Little. *Pinus cembroides* var. *remota* now persists on the Balcones escarpment of the Edwards Plateau (near population 14, Fig. 1) about 300 km to the east of the fossil site. I have recently examined a herbarium specimen of *J. ashei* from eastern Brewster County, Texas and have indicated this location in Fig. 1 (dashed lined population, about 150 km west of population 26). This new population is just north of Wells's (1966) Maravillas Canyon rat midden site. Perhaps his juniper twigs should be reexamined for the presence of *J. ashei*. In any case, this western-most disjunct population of *J. ashei* seems to be of the same relict nature (on preliminary morphological examination) as populations 12, 13, 25, and 26.

Although I have previously considered populations 12, 13, 25, 26, and 17 to be ancestral (Adams, 1975a), one might ask why these might not be advanced, with the central Texas-Ozark populations being ancestral. Examination of Table 4 reveals the significant morphological differences between populations 12, 13, 17, 25, 26, and the other populations. The following characters show significant differences: female cone diameter (smaller in 25, 26, etc.); seeds per cone (generally more in 25, 26, etc.); seed area (smaller in 25, 26, etc.); whip leaf gland area (larger in 25, 26, etc.); whip leaf gland length/width (more elongated in 25, 26, etc.); whip leaf gland length/sheath length (larger in 25, 26, etc.); and branching angle (larger in 25, 26, etc.). Reviewing the *Sabina* section of *Juniperus* in North America, it seems that some of these character states are rather unusual and are likely advanced (rather than primitive). Advanced character states (central Texas-Ozarks) are: larger female cones concurrent with fewer seeds (just the opposite found in most of the junipers); whip leaf gland area small (whip leaf gland area is generally large in junipers where the glands are visible); whip leaf gland length/width close to 1 or 1.5 (*J. ashei* is unique in the genus, so far as is known, in having raised, round glands), the more elongated glands (populations 25, 26, etc.,) are definitely the more primitive type; and whip leaf gland length/sheath length (almost always large in *Juniperus*, except the central Texas-Ozark *J. ashei*). Advanced and primitive states are not known for two characters: seed area and branching angle. Overall, the characters expressed in central Texas and the Ozarks are generally unusual in occurrence



CHEM. SR, ASHEI-SALTILLENSIS



MORPH. SR, ASHEI-SALTILLENSIS

FIGURES 12–13.—12. The contoured F-1 weighted morphological similarity of each population of *J. ashei* to *J. saltillensis*, collected near Saltillo, Mexico. *Juniperus saltillensis* is thought to be closely related to the ancestral stock of *J. ashei*. Notice the clinal differentiation from west Texas to the Mexico population (25). Contours: 1 = 0.16; 7 = 0.46.—13. The contoured F-1 weighted terpenoid similarity of each population of *J. ashei* to *J. saltillensis*. The clinal trend seen with the morphology (Fig. 12) is steeper in the terpenoids, and population 17 is obviously more closely related to the ancestral stock of *J. saltillensis-J. ashei*. Contours: 1 = 0.17; 7 = 0.41.

in *Juniperus* compared to the character states found in the southwest Texas-Mexico populations. Further evidence regarding the ancestral nature of populations can be obtained by comparison of each population of *J. ashei* with its presumed nearest ancestor (Zanoni & Adams, 1976), *J. saltillensis* Hall. Although *J. ashei* probably did not descent from *J. saltillensis*, that taxon appears to bear the closest morphological and terpenoid similarities to *J. ashei* of any in North America. In Fig. 11 I have constructed differential similarities of each population of *J. ashei* to a sample of 15 trees of *J. saltillensis* from near Saltillo, Mexico. ANOVA was performed on 29 data sets (28 *J. ashei* populations and 1 *J. saltillensis* population) to determine a set of F-1 weights. Similarity measures were calculated as outlined before, then each population of *J. ashei* was contour mapped showing the change (differential) in similarity to *J. saltillensis* (the geographical source of this taxon is not important for obtaining the similarities and is not shown on the maps). This method of "differential similarity" should prove very useful in the analysis of the interaction of two species across a geographical area. Figure 12 is based on 15 morphological characters (female cone color omitted, F = 0.88), F-1 weighted. Notice that the highest similarity to *J. saltillensis* is from the Mexico population (25), followed by populations 26, 12, 13, and 17. The knife edge break previously seen (Fig. 4) between populations 12, 13 and 11, 14 is quite widened in this analysis with a cline from populations 12 to 10. The Post population (24) bears some similarity, but part of this similarity may be due to environmental factors.

The terpenoids of *J. ashei* are interesting evolutionarily because there is a

greater shift toward the predominance of a single compound (camphor, see von Rudloff, 1968; Adams & Turner, 1970) than in any other member of the genus. In populations of central Texas camphor averages about 75% of the total oil (2 hr. extraction) whereas the divergent populations average about 60%. *Juniperus ashei* has by far the simplest oil mixture of the North American junipers, and this seems to be an advanced character state of specialization. The central Texas populations are particularly low in the sesquiterpene oxygenated compounds such as elemol, elemol-acetate, and α, β and γ-endesmols. Larger quantities of these compounds are the rule in the rest of the junipers and conifers in general (see von Rudloff, 1975).

Differential similarities, based on ANOVA (28 *J. ashei* populations plus 1 *J. saltillensis* population) and using 68 terpenoids F-1 weighted, reveal (Fig. 13) a pattern almost identical to the differential similarities for the morphological characters (Fig. 12). These similarities indicate that the divergent populations (25, 26, 12, 13, 17) bear a stronger affinity to *J. saltillensis* than the central Texas-Ozark populations (lest the reader be suspicious of mixed sampling in population 25, etc., I should note that these divergent populations clustered strongly with the central Texas type when an OTU of *J. saltillensis* was added to the matrix set, and intrapopulational cluster analysis of each of the 28 populations of *J. ashei* revealed no other taxa as would be the case in mixed species samples). Thus we see that in considering a fairly large set of characters (15 morphological and 68 terpenoids), the dominant theme is for the divergent populations to be progressively more similar to *J. saltillensis*. It should be noted that *J. saltillensis* is not conspecific with *J. ashei* (Zanoni & Adams, 1975, 1976). In fact, several characters found in *J. saltillensis* (curved terminal whips and beady scale leaves) have not been found, even in the relict populations, in *J. ashei*. Although relict hybridization could not be conclusively ruled out at present, it seems unlikely since we have no direct evidence that the two taxa have been sympatric, and several distinguishing characters of *J. saltillensis* have not been found in divergent *J. ashei* plants. It would appear that the most probable hypothesis at present is that *J. ashei* and *J. saltillensis* had a common ancestor (Tertiary?) in the Sierra Madre Oriental. *Juniperus ashei* differentiated and migrated northeastward to the exposed limestone outcrops (Edwards Plateau, Arbuckles, Ozarks, etc.), while *J. saltillensis* adapted to the drier, interior portion of the Sierra Madre Oriental.

During the Pleistocene ice advances, *J. ashei* may have become extinct in Missouri, Arkansas, Oklahoma, and most of central Texas as depicted in Fig. 14. During the same period, *J. ashei* probably expanded westward into the current Chihuahuan desert (Wells, 1966; Bryant, 1969), but not as far south as Cuatro Cienegas (Meyer, 1973). Migration west of the Sierra del Carman was also possible since the species is currently found at the top of a pass (La Cuesta) just south of the Sierra del Carman. Whether *J. ashei* could have crossed the high plateau around Alpine and Marfa (1,500 m) is not known, but suitable habitat was probably available for colonization in the Presidio area. With this model, populations of *J. ashei* would be forced to extinction in central Texas, Oklahoma, Arkansas, and Missouri. The subsequent recolonization could then take place

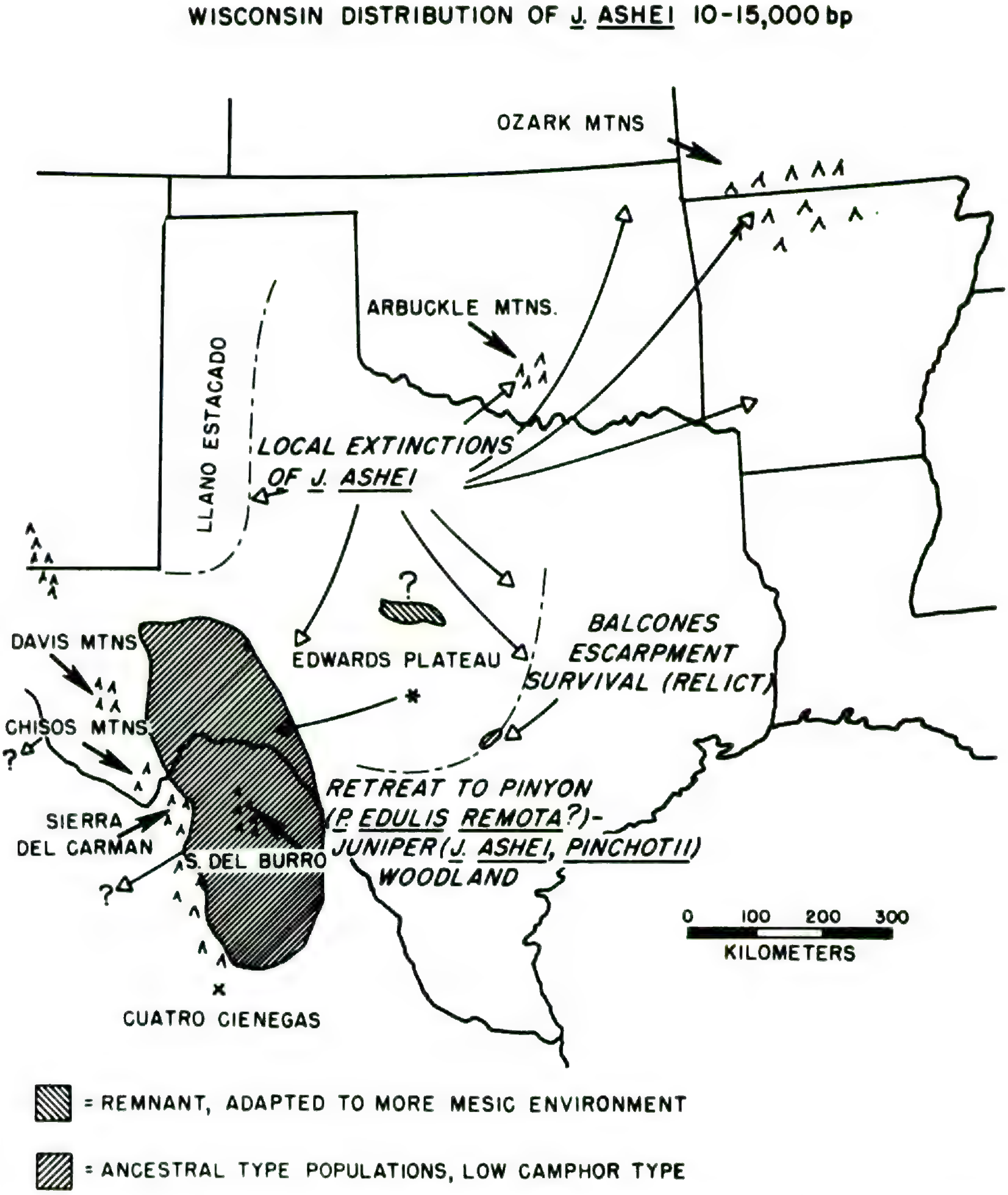


FIGURE 14. Possible Wisconsin distribution of *J. ashei,* 10,000–15,000 B.P. Following the advance of subalpine and montane species (Fig. 11), *J. ashei* populations may have gone extinct north of the Edwards Plateau. See text for discussion.

according to Fig. 15 over a very short period of time (hundreds of years?) from some population in central Texas that may have gone through a selection "bottleneck," perhaps coupled with genetic drift. This "relict" population would have had considerably more camphor in the oil (as a plant defense?), more roundish glands, larger female cones, fewer seeds (therefore a higher pulp to seed ratio for bird dispersal), and a more lax foliage (smaller branching angle) which seems to be associated with more mesic species. The rapid recolonization of limestone outcrops (Fig. 15) could then lead to a uniform taxon from central Texas through

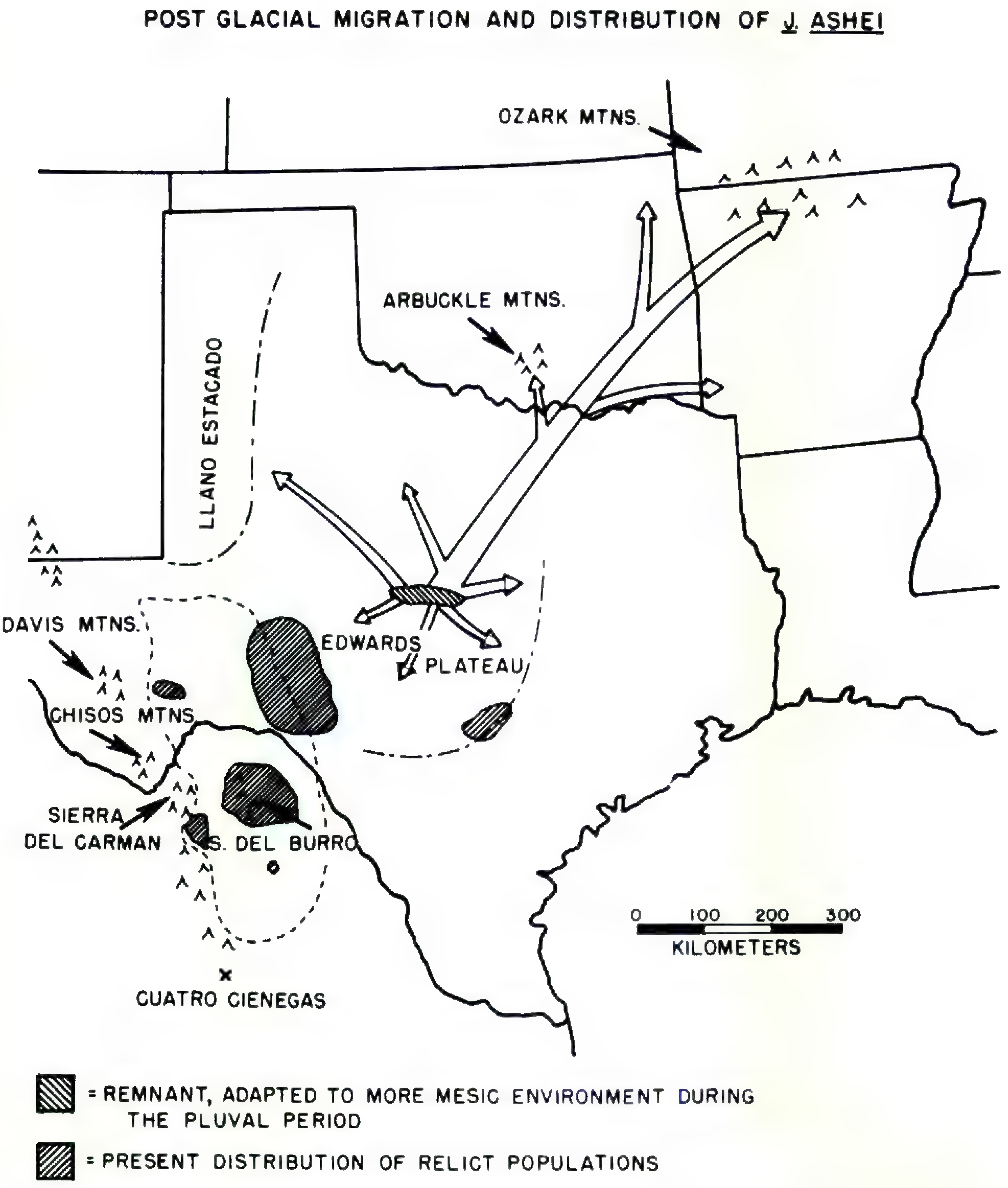
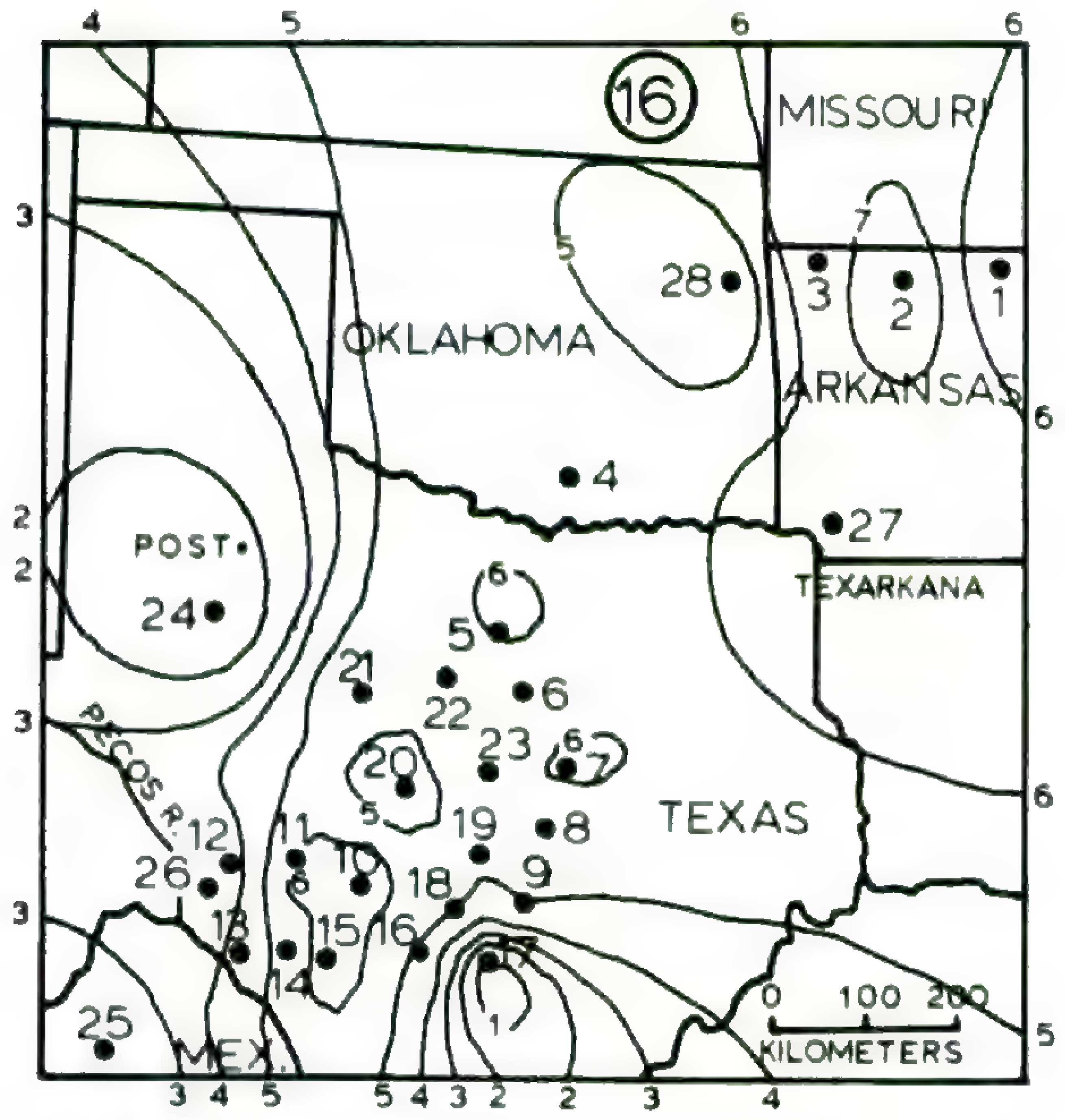
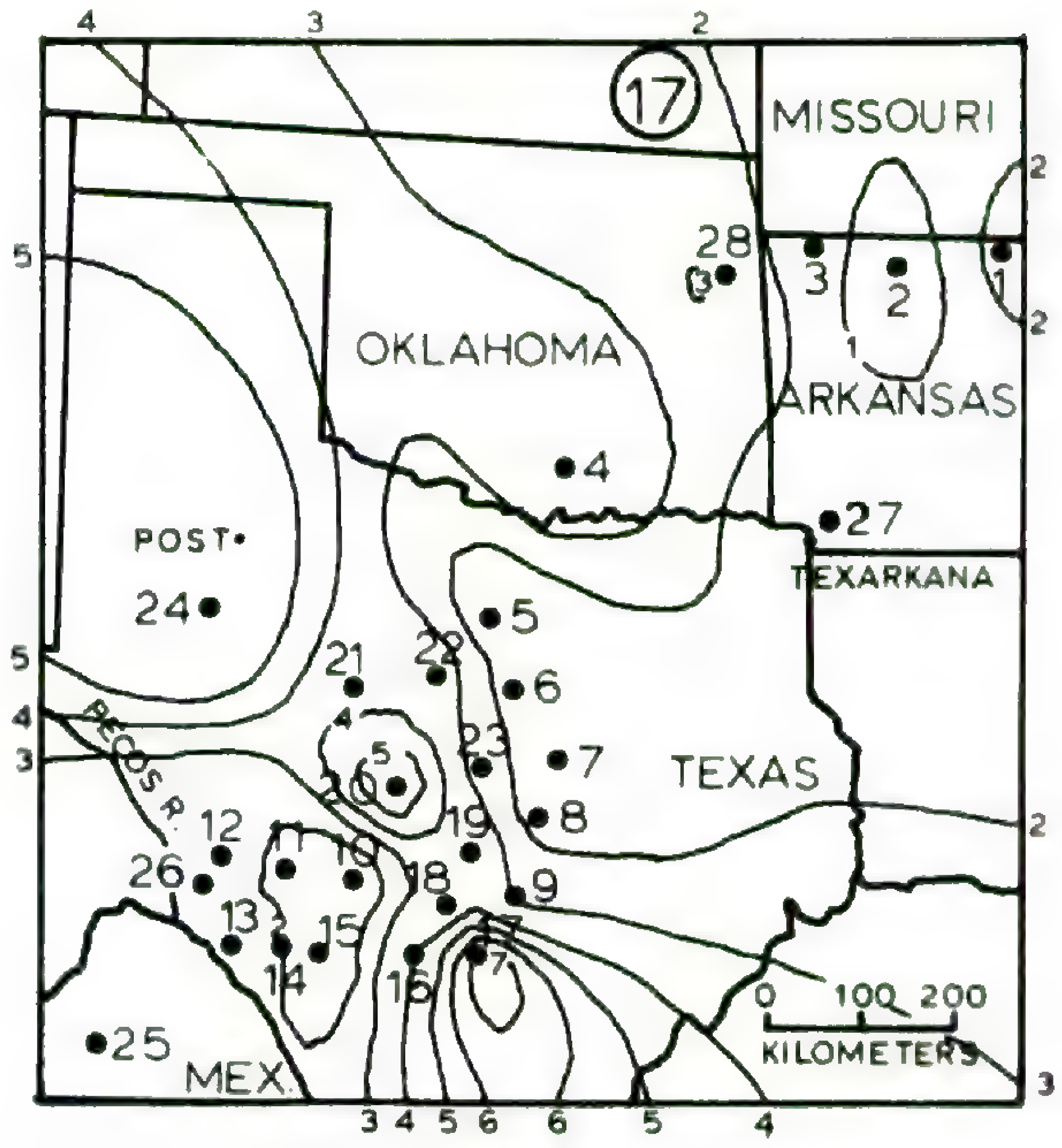


FIGURE 15. Possible post-glacial migration to attain the present distribution of *J. ashei*. The remnant (high camphor type) adapted to a more mesic environment may have quickly expanded during the hypsithermal to reach the present distribution (see Fig. 1). The dashed line shows the pluvial distribution of the ancestral type (lower camphor) populations (see Fig. 14).

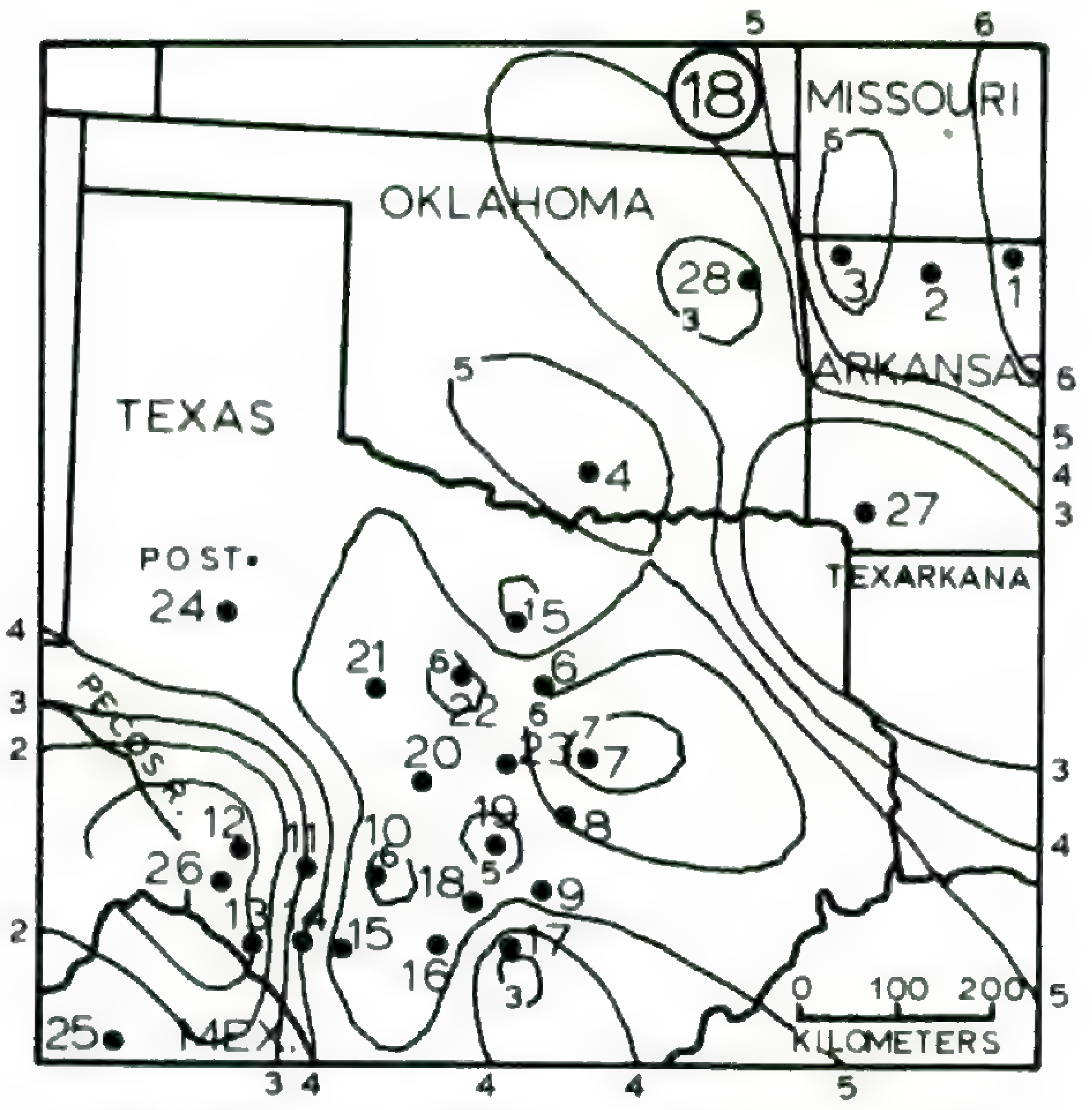
the Ozarks. Although this would explain the observed patterns, many uncertainties remain. For instance, Dillon (1957) argues that the boreal forest elements were merely mixed with the present floral components in the southern states. Graham (1973) feels that most central-southern communities incorporated boreal elements (e.g., spruce) but retained the general character of the original vegetation. If small pockets of *J. ashei* did persist during the full glacial,



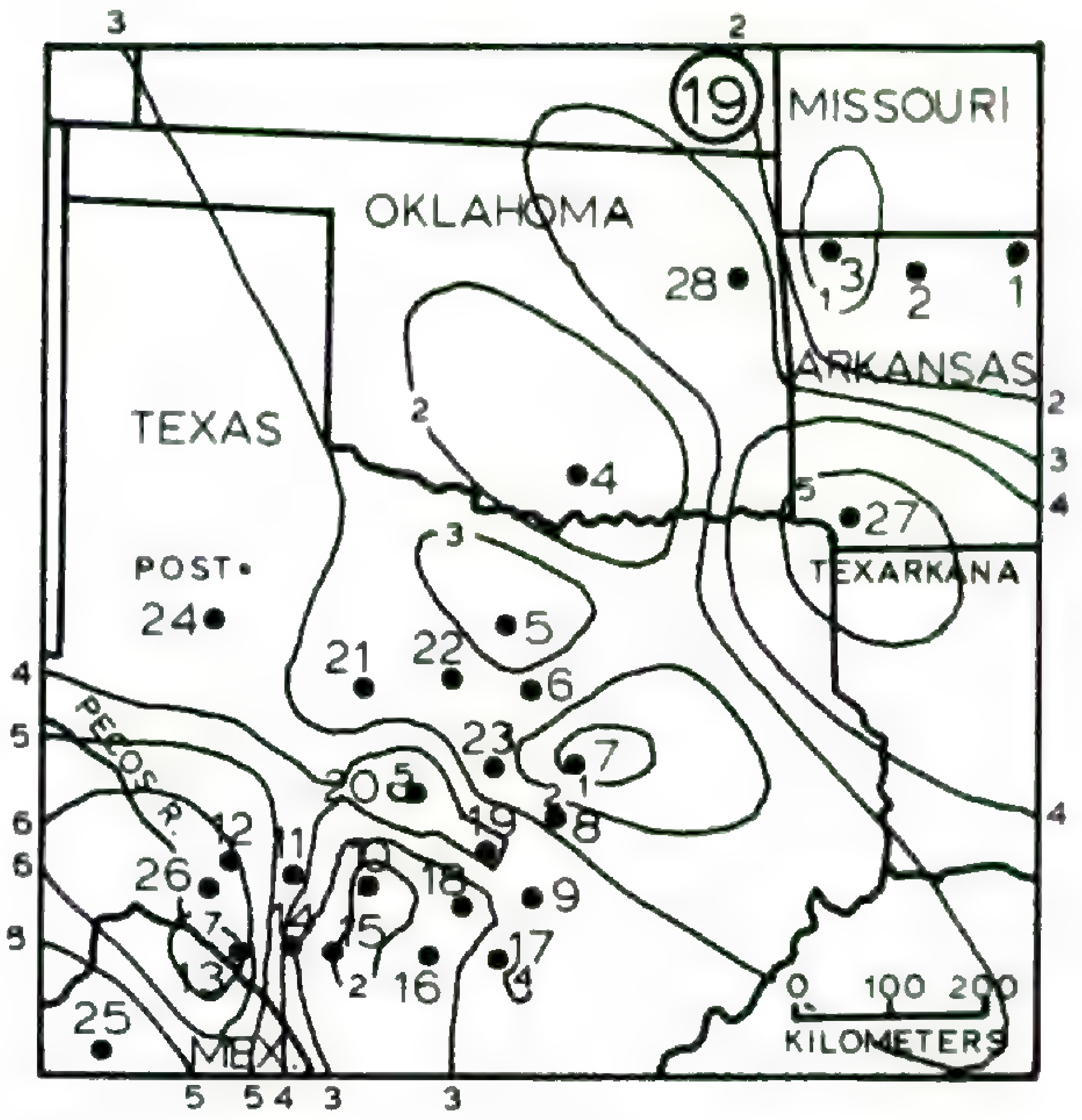
AVG. SIMILARITY, TERPENOIDS



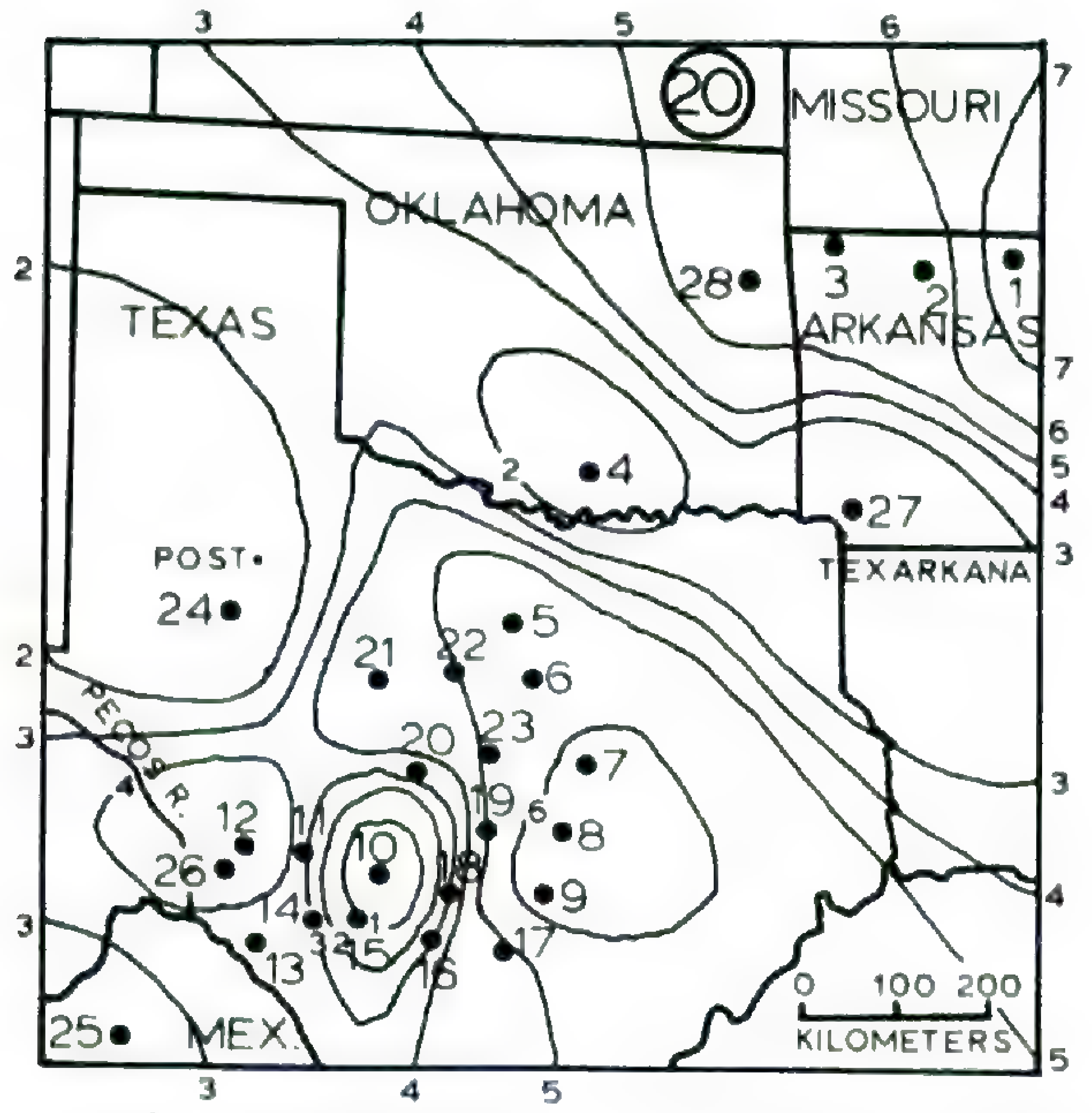
CPV, TERPENOIDS



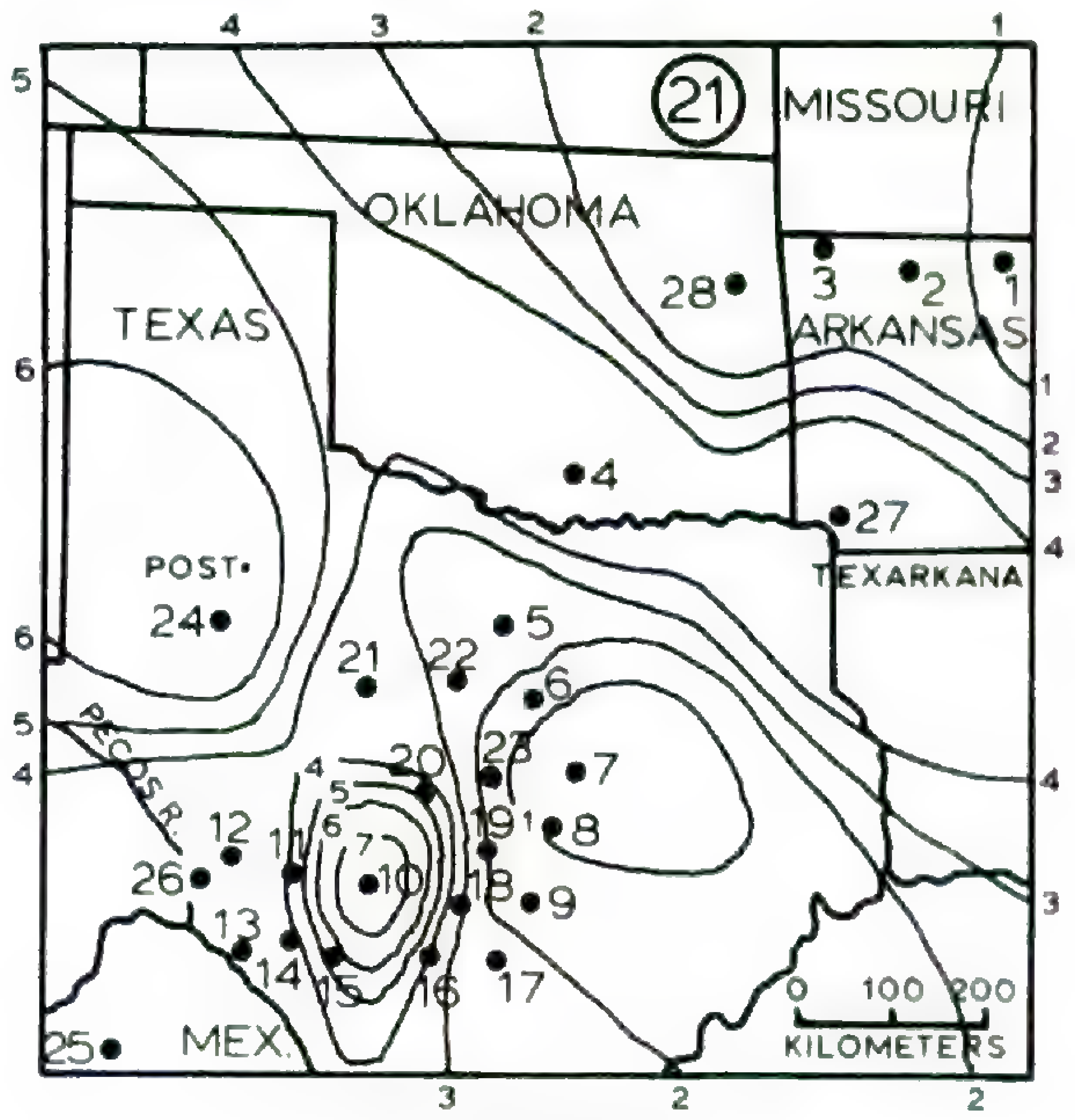
AVG. SIMILARITY, MORPHOLOGY



CPV, MORPHOLOGY



AVG. SIMILARITY, PEROXIDASES



CPV, PEROXIDASES

one might find some evidence of this based on intrapopulation variability, with the smaller Pleistocene relictual populations having less variability than larger (south-central Texas) populations.

Intrapopulational Variability

Mean similarity ($\overline{Sr}$) within each population (15 trees) for 152 terpenoid characters (W = 1) shows high average similarities in the Ozarks and central Texas (10, 11, 15) and low similarities at New Braunfels (17), Post (24), and Mexico (25). The divergent populations (12, 13, 17, 25, 26) tend to be a little less uniform, although Post (24) is also quite variable. Populations that showed the major trend of the terpenoids (Fig. 3) tended to be uniform. Examination of the homogeneity of the similarities was accomplished by computing the standard deviation of the mean similarity and dividing by the mean similarity of that population for normalization (CPV). The most homogeneous similarities are in the Ozarks (2, 3) and central Texas (10, 15, 7), whereas the least homogeneous are New Braunfels (17), Brady (20), and Post (24). The populations which showed the highest similarities are the most homogeneous except for population 20 (Brady). The low similarities and lack of homogeneity at New Braunfels seems to be due to the interaction between relict and modern genotypes. One might question if the population at Post (24) is hybridizing with sympatric *J. pinchotii* trees but notice the close ordination of 24 with the central Texas *J. ashei* (Fig. 3). Examination of the intrapopulation phenogram revealed no major groups within any population.

Analysis of 16 morphological characters (W = 1) shows the highest similarities in central Texas (7, 10, 18) and the Ozarks (1, 3), with lowest similarities in the relict populations (12, 13, 26, 17, 25) and at Texarkana (27). Two small island populations (27, 28) both show considerably lower similarities in their morphology than they did in their terpenoids, whereas Post (24) is more medial in its morphological similarities than with the terpenoids (Fig. 16). The CPV

←

Figures 16–21.—16. Average similarity ($\overline{Sr}$) within each population (15 trees) based on 152 equally weighted terpenoids. Most populations had high internal similarities with the exception of the ancestral populations (12, 13, 17, 25, 26) and the Post population (24). Contours: 1 = 0.78; 7 = 0.87.—17. Contoured coefficient of phenetic variation (CPV) of the terpenoid similarities. In general the populations with high intrapopulation similarities were homogeneous (low CPVs) and vice versa, except for population 20 which had high similarities and was not so homogeneous (high CPV). Contours: 1 = 0.30; 7 = 0.91.—18. Average similarity within each population based on 16 equally weighted morphological characters. Note that the ancestral populations are of generally lower internal similarities compared to high similarities throughout central Texas. The small populations at Texarkana and northeastern Oklahoma are morphologically quite variable. Contours: 1 = 0.85; 7 = 0.91.—19. Contoured coefficient of phenetic variation (CPV) of the average morphological similarities. The CPV seems highly negatively correlated with the mean Sr except for populations 19 and 20 which are not very homogeneous. Contours: 1 = 0.28; 7 = 0.60.—20. Contoured average similarities of 23 equally weighted peroxidases. The Junction population (10) had the lowest similarities along with Post (24) and the Arbuckles (4). Contours: 1 = 0.54; 7 = 0.96.—21. Contoured coefficient of phenetic variation of the peroxidase similarities gives an almost identical pattern as seen in the average similarities (Fig. 20). Contours: 1 = 0.13; 7 = 0.32.

gives a fairly similar pattern of homogeneity except for populations 19 and 20, which, although very typical (Fig. 4) and of high average similarities, are not very homogeneous. This same phenomenon was seen with the terpenoids (Figs. 3, 16–17) for populations 19 and 20. The Post (24) population is somewhat more homogeneous in its morphology than its terpenoid's similarity. With the exception of populations 24 and 27, one notices that for each of these four statistics, the populations generally present some trend of variability which is correlated with either regional differentiation or proximity of one population to another (the case for 19 and 20).

All 23 peroxidase electromorphs were subjected to the computation of average similarities within population and CPVs, as with the morphology and terpenoids. Only the 15 populations marked with an asterisk in Figs. 20 and 21 have isoperoxidases analyzed. The average similarities within populations for these 23 isozymes show the Ozark population (Fig. 20) to be quite similar (0.97–0.80), while the Junction, Texas population (10) has the lowest average similarity (0.47). A surprising aspect of these average similarities is the low average similarity found in population 10 (Junction, Texas). It is interesting that 3 different peripheral populations (1, 27, 24) show the whole range of variation from little to large amounts to intermediate variability. The CPV (Fig. 21) of these 23 peroxidases reveals that those populations that are highly similar are generally most homogeneous and vice versa. A combined total of 43 isoenzymes has been analyzed by Kelley & Adams (1977b), and the results are comparable to those shown in Figs. 20 and 21. However, the addition of 14 alcohol dehydrogenases and 4 esterases to the analysis seemed to have produced a slightly less mosaic pattern in central Texas.

The pattern obtained from the isoenzymes is quite different from either the morphology or terpenoids for in both of those analyses, population 10 appeared to be quite uniform and homogeneous and the relict populations consistently displayed high to medium variability. It seems apparent that whatever variability the peroxidases are indicating, it is not directly related to variability in the morphology nor terpenoids. Of course, it is possible that the variation seen in peroxidases is below the level of selection and merely represents "random noise." Until more information is gathered on the selection value of various electromorphs, we can only speculate.

The patterns of variability seem to give us a few clues as to whether the disjunct populations are of recent origin or relicts of the advanced high camphor types. However, presently it is difficult to make generalizations about populational variability versus founder's effect, "bottlenecks," relictness, etc. since different character sets give somewhat (to vastly) different answers, and one could get the same observed pattern depending on time, microselection intensity, or site variability.

CONCLUSION

Treating peroxidase data as qualitative taxonomic chemical characters did not appear to be feasible. This is likely due to the lack of homology, intense microhabitat selection or random (neutral) variations in the electromorphs.

The use of these peroxidase electromorphs for the analysis of intrapopulation variability could not be readily evaluated due to the mosaic pattern produced. It appears that chemosystematists will need more detailed biochemical information about the nature of isoenzymes, and their genetic control in taxa to be studied.

The most probable center of origin for the modern (high camphor) populations of *J. ashei* seems to be in central Texas, perhaps near Brady (20) or Burnet (19). These populations showed considerable variability (high CPVs), yet these populations are quite similar to the rest of the modern *J. ashei* populations. Northward migrations of birds during the spring carrying juniper seeds could have (re)colonized limestone outcrops in Arkansas, Oklahoma, and Missouri in a span of a few hundred years. This could lead to the highly uniform pattern observed in the morphology and terpenoids from central Texas to the Ozarks. Predominately southerly winds during pollination may have been important in maintaining the north-south split in west Texas as well as the relict population at New Braunfels, Texas (17). However, it is possible that the populations persisted throughout the pluvial periods and failed to diverge due to either a lack of variability, the relatively short time span involved, or intense selection for the modern phenotype.

Whether the modern populations of this taxon invaded the limestone outcrops in the Tertiary or during the Pleistocene will probably not be known until some pollen or macrofossil (rat midden) data has been analyze in the disjunct populations of Arkansas, Missouri, and Oklahoma. The differential similarity of *J. ashei* population to *J. saltillensis* from Saltillo, Mexico shows a clear trend of past (Pleistocene) migration from northern Mexico. The northern Mexico Sierra Madre Oriental seems a likely site for the origin of both *J. ashei* and *J. saltillensis*, perhaps from a common ancestor.

This study presents additional evidence that selection may be more important than gene flow (Ehrlich & Raven, 1969) in the maintenance of species. In *J. ashei* we have found that populations with disjunctions of 200–300 km, and a trivial chance for gene exchange, were very similar to other populations covering 1,000 km of range (cf. Ozarks and central Texas populations). Yet populations which are in close (almost continuous) proximity have maintained either ancestral or modern patterns in spite of potentially large amounts of gene flow. (New Braunfels and populations to the north and west, and the relict/modern populations of west Texas).

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THE ORDER CENTROSPERMAE[1]

Tom J. Mabry[2]

Abstract

Perhaps no other order of flowering plants of its size is as well investigated morphologically, ultrastructurally, and chemically as is the Centrospermae. The betalain pigment discoveries of the early 1960s were followed by the more recent discovery of unique protein depositions in the sieve-element plastids of members of this order. These and other molecular data, including DNA-RNA hybridization results, have permitted a circumscription of the order based on 11 core families, including all 9 betalain families: Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Chenopodiaceae, Didiereaceae, Nyctaginaceae, Phytolaccaceae, and Portulacaceae, as well as two anthocyanin families: Caryophyllaceae and Molluginaceae. Several smaller betalain taxa (including *Gisekia*, *Halophytum*, *Hectorella*, and *Dysphania*) which are sometimes treated as independent families or as members of one of these 11 core families also clearly belong to the order. Other families such as the Bataceae, Gyrostemonaceae, Vivaniaceae, and Theligonaceae are excluded from the Centrospermae. The betalain evolutionary line of centrospermous families may have originated from a centrospermous ancestor which lost the ability to produce anthocyanins and then subsequently gained the two or three steps required to produce betalains. Pollen morphology of centrospermous taxa and the widespread occurrence of C_4 photosynthesis in the Centrospermae are also discussed.

Since all the review papers from a symposium on the "Evolution of Centrospermous Families," presented in July, 1975 during the XIIth International Botanical Congress, Leningrad, USSR, have now been published (Mabry & Behnke, 1976a), a summary of our current views of the Centrospermae (or Caryophyllales) will suffice in this review. This account will emphasize the way our interpretations of the order have been shaped by molecular data.

Since 1876 when Eichler (see Table 1) introduced the name for the order, the Centrospermae have always contained a core of about 8–12 families. Eichler (1876 and, in part, 1878) recognized most of what we now consider to be centrospermous families including, for example, the Cactaceae (in the 1876 treatment). In the 100 years following Eichler's work, most systematists also included those families now generally recognized on the basis of molecular data as belonging to the order but often included additional ones (compare Tables 2, 3 and 4). The molecular data which bear upon our current treatment of the order are summarized in the following sections.

Sieve-element Plastids

Of all the modern approaches for investigating the Centrospermae, none has, in my opinion, contributed more to our understanding of the circumscription of the order than the ultrastructural investigations of the sieve-element plastids.

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TABLE 1. Centrospermae (A. W. Eichler, 1876).

I. Order: Oleraceae	III. Order: Opuntinae
1. Polygonaceae	6. Phytolaccaceae*
2. Nyctaginaceae*	7. Portulacaceae*
3. Chenopodiaceae*	8. Aizoaceae*
4. Amaranthaceae*	9. Cactaceae*
II. Order: Caryophyllinae	(? In this Order perhaps Begoniaceae)
5. Caryophyllaceae	

* Betalain families.

The discovery by Behnke that the nine core betalain families (see Table 4) as well as the two core anthocyanin families (the Caryophyllaceae and Molluginaceae) contain ringlike inclusions composed of proteinaceous filaments of a type (Fig. 1) not found elsewhere in the angiosperms (for current reviews, see Benhke, 1976a and in press) established that these eleven families represent the core centrospermous families. Behnke (in press) defined the sieve-element plastids which are unique to the Centrospermae as belonging to the P-III subtype. It is my current view that the presence of the P-III subtype sieve-element plastids in a taxon which classical data suggest might be centrospermous (see Eckardt, 1976 for comments on centrospermous characters) establishes that it belongs to the Centrospermae.

C_4 Photosynthesis in the Centrospermae

It is interesting that among the dicotyledons which have the C_4 photosynthetic pathway (the Kranz syndrome), 7 of the 11 families (Table 5) and about 85% of the genera have been reported among the Centrospermae (Walter Brown, private communication). It is perhaps significant that the Phytolaccaceae, which most workers consider to be the basal family of the order, exhibits only the C_3

TABLE 2. Caryophyllidae (Cronquist, 1968).

I. Order Caryophyllales	II. Order Batales
1. Phytolaccaceae* (incl. Achatocarpaceae, Agdestidaceae*, Barbeuiaceae, Gyrostemonaceae, Petiveriaceae*, Stegnospermaceae*)	1. Bataceae
2. Nyctaginaceae*	III. Order Polygonales
3. Didiereaceae*	1. Polygonaceae
4. Cactaceae*	IV. Order Plumbaginales
5. Aizoaceae* (incl. Mesembryanthemaceae*, Tetragoniaceae*)	1. Plumbaginaceae
6. Molluginaceae	
7. Caryophyllaceae (incl. Illecebraceae)	
8. Portulacaceae*	
9. Basellaceae*	
10. Chenopodiaceae (incl. Dysphaniaceae*, Halophytaceae*)	
11. Amaranthaceae*	

* Betalain families.

TABLE 3. Caryophyllales, Polygonales and Plumbaginales (Takhtajan, 1973).

27. Ordnung. Caryophyllales
   1. Phytolaccaceae* (incl. Achatocarpaceae, Agdestidaceae*, Barbeuiaceae, Petiveriaceae*, Stegnospermaceae,* excl. (?) *Rhabdodendron*
   2. Gyrostemonaceae
   3. Bataceae
   4. Nyctaginaceae*
   5. Molluginaceae (incl. Gisekiaceae*)
   6. Aizoaceae*
   7. Tetragoniaceae*
   8. Cactaceae*
   9. Portulacaceae*
   10. Basellaceae*
   11. Didiereaceae*
   12. Halophytaceae*
   13. Hectorellaceae*
   14. Caryophyllaceae (incl. Illecebraceae)
   15. Vivianiaceae
   16. Amaranthaceae*
   17. Chenopodiaceae* (incl. Dysphaniaceae*)

28. Ordnung. Polygonales
   Polygonaceae

29. Ordnung. Plumbaginales
   Plumbaginaceae (incl. Armeriaceae)

* Betalain families.

pathway. Although the C_4 pathway probably represents a derived condition as taxa of the order radiated into xeric and other high light intensity habitats, it is likely that some form of preadaptation for the Kranz syndrome exists throughout the order. This preadaptation has permitted repeated and independent evolution of the syndrome at various times and in numerous genera in at least seven families of the order (Walter Brown, private communication). The only other dicotyledonous families exhibiting the C_4 pathway are the Boraginaceae (*Heliotropium* in part), Compositae (7 genera), Euphorbiaceae (*Chamaesyce*), and Zygophyllaceae (3 genera).

It should also be noted that the CAM (crassulacean acid metabolism) photosynthetic pathway occurs in members of the Cactaceae and Aizoaceae; this pathway, although anatomically, functionally and phylogenetically distinct, does utilize enzymes of the Kranz syndrome. Although CAM plants are photosynthetically

TABLE 4. Order Centrospermae[a] or Caryophyllales (modified here from Mabry, 1976). (Taxa with P-III subtype sieve-element plastids.)

SUBORDER CHENOPODIINEAE[b] (BETALAIN FAMILIES)

Aizoaceae (incl. Tetragoniaceae and possibly Gisekiaceae)
Amaranthaceae
Basellaceae
Cactaceae
Chenopodiaceae (incl. Dysphaniaceae)
Didiereaceae
Halophytaceae
Nyctaginaceae
Phytolaccaceae (incl. Achatocarpaceae, Agdestidaceae, Petiveriaceae, Stegnospermaceae)
Portulacaceae (incl. *Hectorella*)

SUBORDER CARYOPHYLLINEAE (ANTHOCYANIN FAMILIES)

Caryophyllaceae
Molluginaceae (excl. *Gisekia*)

[a] Certain families which on occasion have been treated as members of the Centrospermae but are now known to contain neither the Centrospermae-specific sieve-element plastids (subtype P-III) (see Behnke, 1976a, 1976b, in press) nor betalains are excluded from the order: Polygonaceae, Plumbaginaceae, Fouquieraceae (Behnke, 1976b), Frankeniaceae (Behnke, 1976b), *Rhabdodendron* (Behnke, 1976b; remains to be analyzed for pigments), Vivianiaceae (Behnke & Mabry, 1977), Theligonaceae (Mabry et al., 1975), and Bataceae and Gyrostemonaceae. So far neither anthocyanins nor betalains have been detected in the latter two families both of which contain glucosinolates (see Goldblatt et al., 1976 for recent comments on the status of these two families).

[b] Whether or not such betalain taxa as *Petivera* and *Agdestis* (Behnke et al., 1974), *Halophytum* (Hunziker et al., 1974), *Gisekia* (Mabry, Behnke & Eifert, 1976), *Dysphania* (Mabry & Behnke, 1976b) and *Hectorella* (Mabry, preliminary results) should each be treated as families in the suborder Chenopodiineae or as members of one of the core betalain families is not resolved.

TABLE 5. Kranz and CAM Photosynthesis[a] in the Order Centrospermae[b] (data from Walter Brown, private communication, 1976).

Suborder Chenopodiineae (Betalain Families)		Suborder Caryophyllineae (Anthocyanin Families)	
Aizoaceae	Kranz and CAM	Caryophyllaceae	Kranz
Sesuvieae	Kranz	Lychnideae	C_3
Gisekiaceae	Kranz	Polycarpeae	Kranz (1 genus)
Tetragoniaceae	C_3	Paronychieae	C_3
Amaranthaceae	Kranz (11 genera)	Diantheae	C_3
Basellaceae	C_3 (3 genera)	Alsineae	C_3
Cactaceae	CAM	Sperguleae	C_3
Chenopodiaceae	Kranz (31 of 67 genera)	Molluginaceae	Kranz (2 genera)
Dysphaniaceae	C_3		
Nyctaginaceae	Kranz (3 genera)		
Phytolaccaceae	C_3		
Achatocarpaceae	C_3		
Agdestidaceae	C_3		
Petiveriaceae	C_3		
Stegnospermaceae	C_3		
Portulacaceae	Kranz (1 genus)		

[a] Kranz = C_4 photosynthesis; CAM = crassulacean acid metabolism pathway.
[b] Not yet examined: Didiereaceae, Hectorellaceae and Halophytaceae. (Added in proof: Didiereaceae and Halophytaceae are C_3.)

inefficient, they are efficient at conserving water (see, for example, Winter, 1974) since they, unlike C_3 and C_4 plants, have their stomata open only at night.

In contrast, Kranz plants have probably been selected for efficient photosynthesis since they, unlike C_3 plants, have evolved an anatomy and enzymatic system which permits them to provide the Calvin cycle with high levels of CO_2 in an oxygen-deficient atmosphere. In the presence of low oxygen concentrations the enzyme which fixes CO_2 in the Calvin cycle, ribulose diphosphate carboxylase oxygenase, is free to function strictly as a carboxylase; therefore under these conditions and with high CO_2 levels and high light intensities, CO_2 fixation is apparently maximized. Thus the reasons for selection of the Kranz syndrome in the Centrospermae (and elsewhere) may be associated in part with evolution in habitats of high light intensity, which, of course, includes many of those which are xeric. Other factors such as salinity also may be important for the selection of C_4 and CAM photosynthesis. In any case, the widespread occurrence of the Kranz syndrome in both betalain and anthocyanin centrospermous families and its sporadic and limited occurrence in other dicotyledons supports current treatments of the Centrospermae (see Table 4) and provides additional evidence that the Centrospermae is an old, independent evolutionary line in the angiosperms.

PIGMENT DICHOTOMY AND DNA-RNA HYBRIDIZATION DATA FOR CENTROSPERMOUS FAMILIES

Higher plants usually contain vacuolar red and yellow pigments which are either anthocyanins or betalains (Fig. 2); however, so far as known, the two types of pigments never occur together in the same plant or even in species

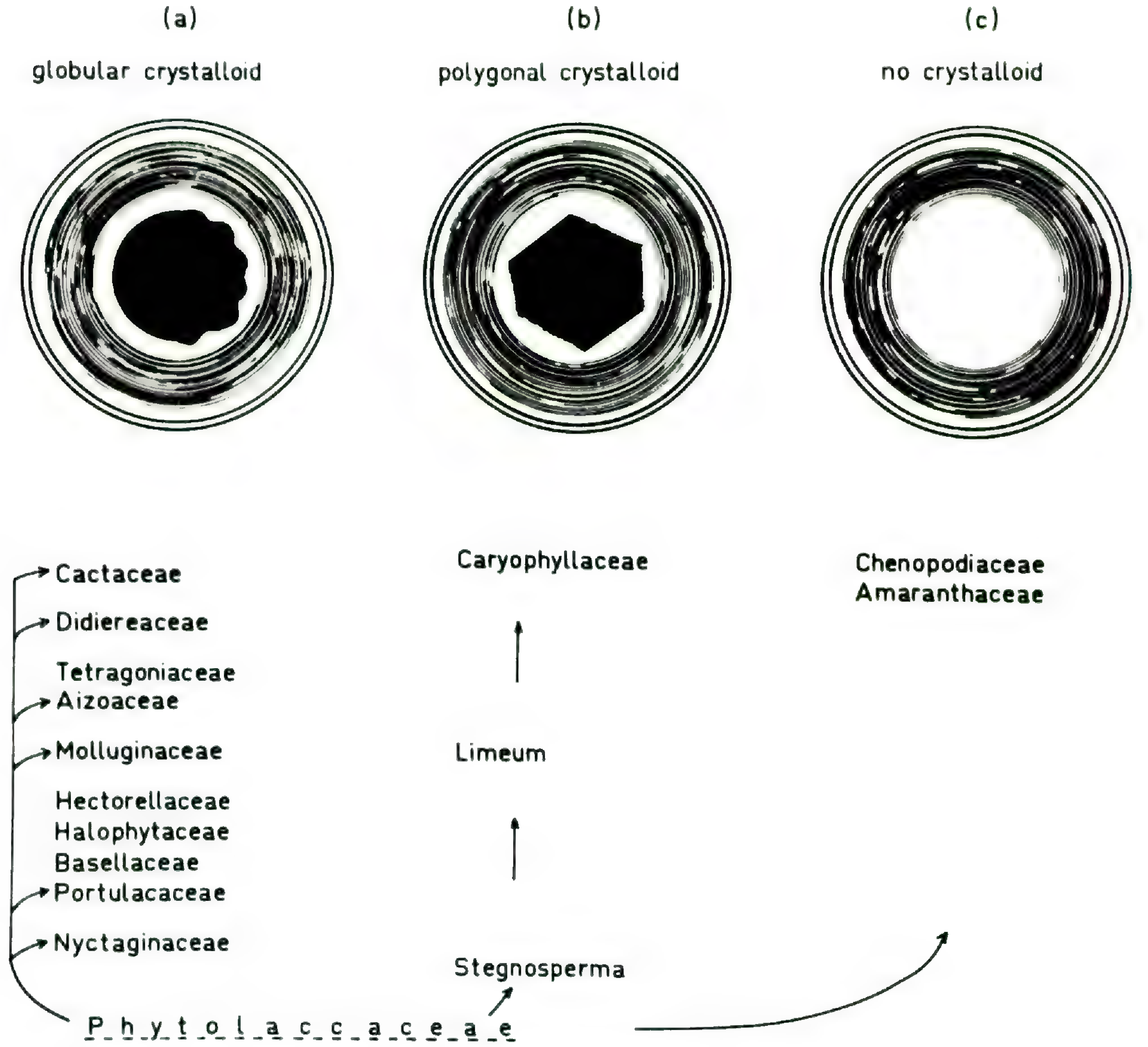

FIGURE 1. The P-III subtype sieve element plastids which are characteristic for the Centrospermae always contain a ring-shaped bundle of protein filaments with either globular (a) or polygonal (b) protein crystalloids or no crystalloid at all (c). I gratefully thank Prof. H.-D. Behnke for this figure which illustrates the distribution of these three modifications of P-III subtype in the Centrospermae.

of the same family. Of these two types, anthocyanins are much more widespread, indeed, they account for most flower pigments in higher plants (for recent reviews of anthocyanins, see Timberlake & Bridle, 1975; Harborne, 1967). In the 1960s it became clear that most centrospermous families contained an entirely new class of red and yellow pigments, designated in 1966 as the "betalains" (Mabry & Dreiding, 1968; for more current reviews, see Mabry, 1973, 1976; Mabry, Kimler & Chang, 1972; Piattelli, 1976). Although we know today that betalains also account for some of the orange and red pigments in many mushrooms, notably species of *Amanita* (Döpp & Musso, 1973, 1974; von Ardenne et al., 1974), these nitrogenous pigments have not yet been reported outside the Centrospermae among angiosperms. It is this restricted distribution of betalains as well as their being mutually exclusive with anthocyanins that makes them interesting as phylogenetic markers.

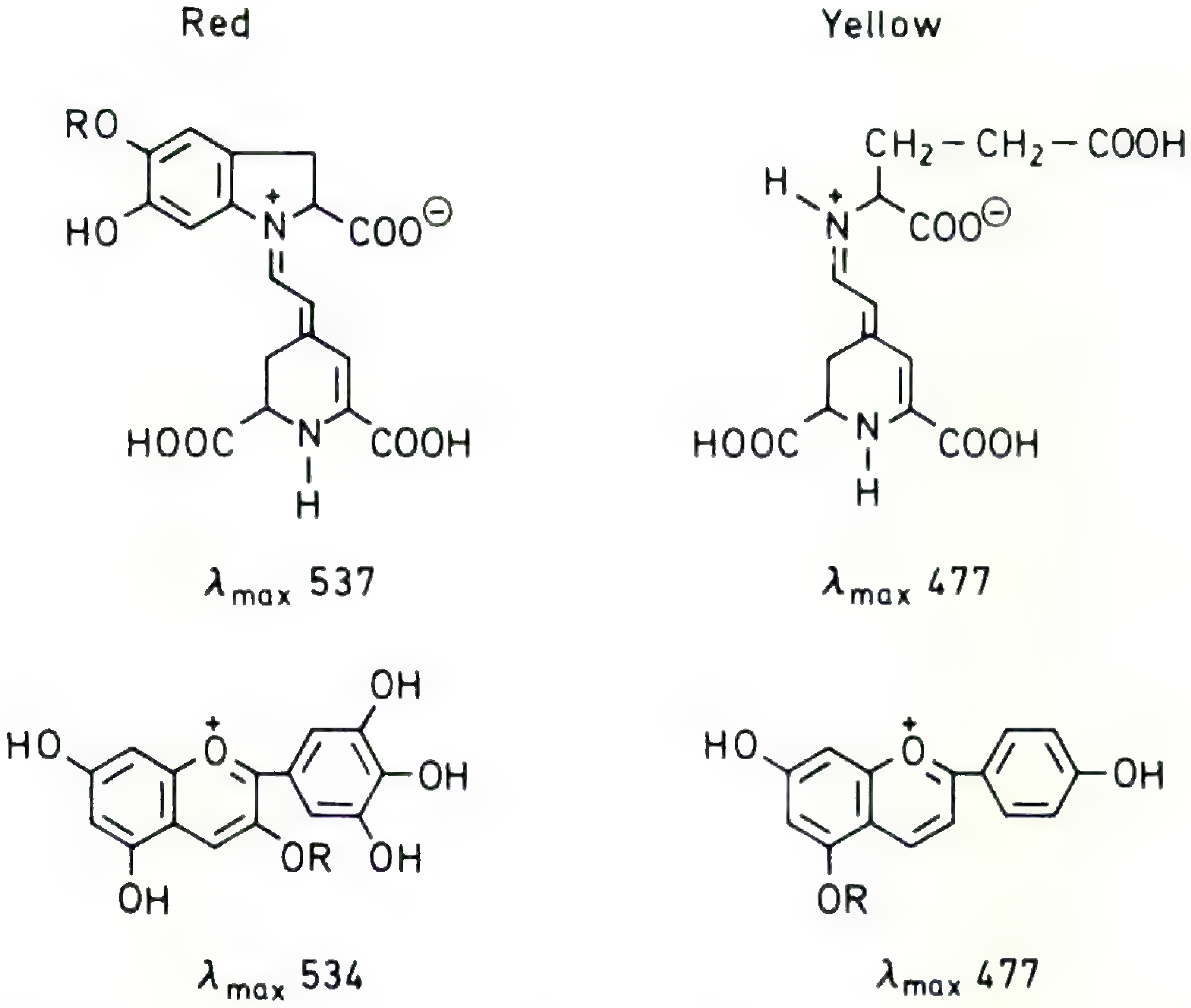

FIGURE 2. The visible absorption maxima of typical red and yellow betalains (top row), which are found only in phyletically related centrospermous families and mushrooms, are similar to those for some red and yellow anthocyanins (bottom row). Anthocyanins account for pigments in most plants, including members of two centrospermous families, the Caryophyllaceae and Molluginaceae.

BIOGENESIS OF BETALAINS

It is the biogenesis of betalamic acid and its subsequent condensation with amino acids and amines which appears to be significant among angiosperms for centrospermous plants. It now appears that the 4,5-extra diol cleavage of L-dopa (Fig. 3) can lead to betalamic acid (Fischer & Dreiding, 1972; Impellizzeri & Piattelli, 1972; Chang et al., 1974) in the Centrospermae and the mushrooms (Musso, private communication) and to stizolobic acid in the anthocyanin-containing Leguminosae (Ellis, 1976) and also mushrooms (Saito et al., 1975, 1976; Musso, private communication). Yet the conversion of the cleaved product to betalamic acid and its conversion into other betalains is known for the Centrospermae and mushrooms only. Whether or not these different groups of organisms utilize the same enzymes to synthesize betalains is not known.

PHYLOGENETIC SIGNIFICANCE OF BETALAINS

Among angiosperms, betalains are known only for centrospermous families, and we use this unique character to circumscribe the suborder Chenopodiineae, order Centrospermae (see Table 4). Whether or not all systematists accept this particular subordinal treatment is not important; it is, however, significant that today the presence of betalains in a family of angiosperms has become a key character used by all workers for its inclusion in the Centrospermae. Such families as the Cactaceae and Didiereaceae were allied with the other betalain

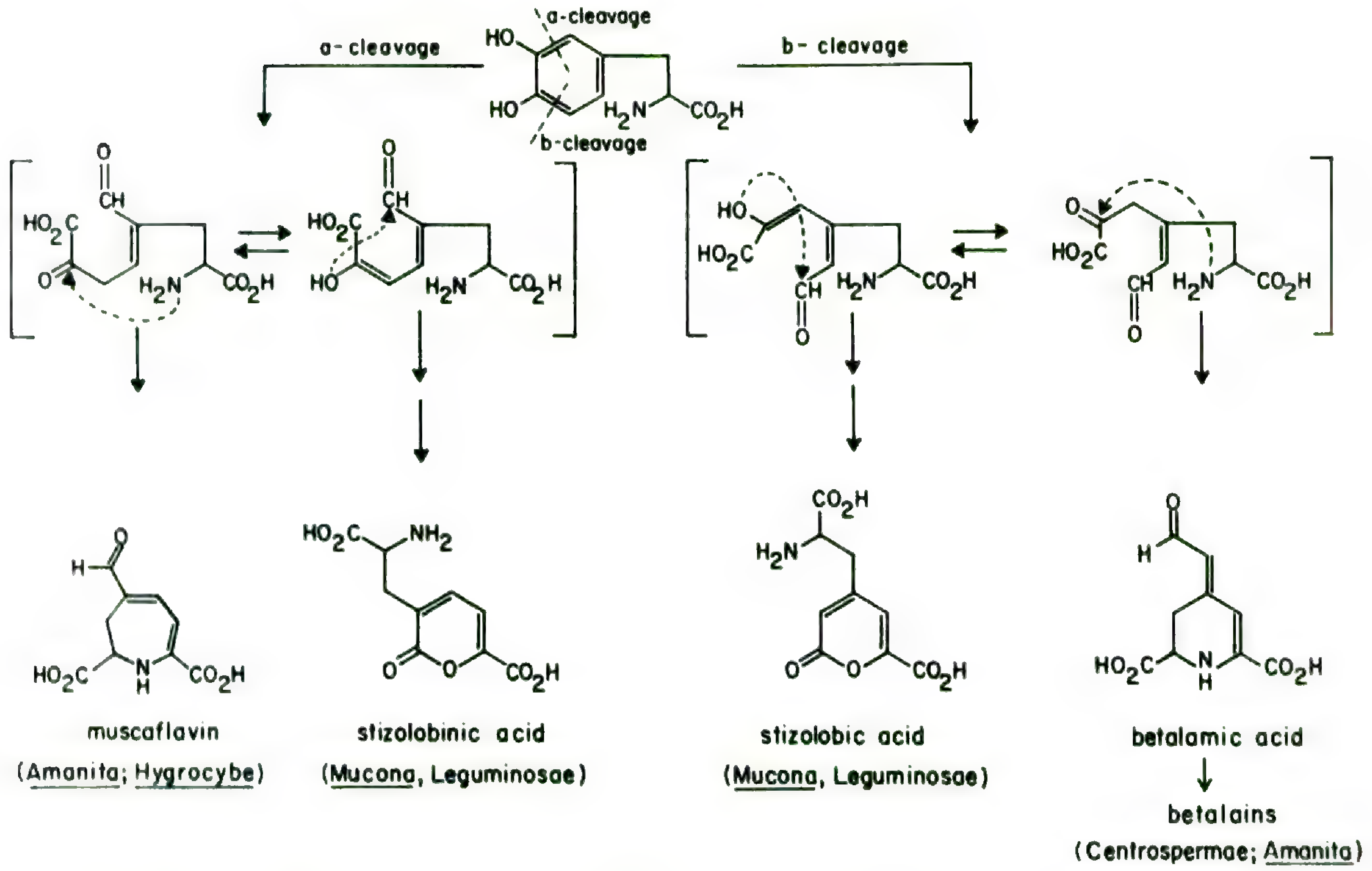

FIGURE 3. L-Dopa is known to undergo 2,3-1 (a-cleavage) or 4,5- (b-cleavage) extra diol cleavage in different organisms. Only in the Centrospermae and in mushrooms does L-dopa lead via the b-cleavage pathway to betalamic acid, the precursor of all other betalains. I thank Prof. H. Musso, Univ. of Karlsruhe, for private discussions which led to the scheme presented here.

families with a greater degree of confidence once their pigments were recognized. Of course, other data such as Jensen's (1965) serological results also firmly established a close relationship of the Didiereaceae to the betalain families, especially the Cactaceae and Portulacaceae.

I suppose over the years the most controversial question has focused upon our 1963 (Mabry, Taylor & Turner, 1963) proposal that the Centrospermae be reserved for the betalain families, with the closely related but anthocyanin-producing centrospermous families (e.g., Caryophyllaceae and Molluginaceae) being placed in a close but distinct order, the Caryophyllales. Although we did not then nor do we now concern ourselves with resolving the question of rank, the separation of the centrospermous families such as the Caryophyllaceae into a separate order "disturbed" a number of leading systematists. Therefore, our current treatment (Table 4), which still maintains distinct taxonomic categories (suborders) for the betalain and anthocyanin families, is more acceptable because all the families are recognized as being "centrospermous." While the phylogenetic importance of the betalains is emphasized in our current treatment, the significance of other characters is recognized. It should be noted once more that our current treatment has been sharply influenced by the occurrence of the same P-III subtype sieve-element plastids in the Caryophyllaceae and Molluginaceae as are found in the betalain families. Despite having our views shaped by different kinds of data, the views of myself and many leading systematists are converging towards a common interpretation of the Centrospermae.

TABLE 6. Pollen Morphology (Nowicke, 1975).

Taxa with Centrospermae-Specific Pollen: Spinulose and Tubuliferous/Punctate Ektexine	Some Taxa with Noncentrospermous Pollen
Betalain Families	Achatocarpaceae
Aizoaceae	Bataceae
Amaranthaceae	Gyrostemonaceae
Basellaceae	Theligonaceae
Cactaceae	Polygonaceae
Chenopodiaceae (incl. Dysphaniaceae)	
Didiereaceae	
Nyctaginaceae	
Phytolaccaceae	
Portulacaceae	
Anthocyanin Families	
Caryophyllaceae	
Molluginaceae	

A number of families sometimes treated as being centrospermous but which contain neither the P-III subtype sieve-element plastids nor betalains are now excluded from the Centrospermae proper (see Table 4, footnote a). Although the available molecular data do not suggest an alternative alignment for many of these taxa, this is not the case for the Bataceae and Gyrostemonaceae. DNA-RNA hybridization data bear upon the relationship of the Bataceae to the Centrospermae (Chang & Mabry, 1974). First, these data indicate that the betalain families which were tested are closer to each other than to any other family and that the Caryophyllaceae is the closest family to the betalain group. At the same time, the Bataceae were clearly separated from the Centrospermae on the basis of the available DNA-RNA hybridization data. Moreover, it is significant that Prof. Martin G. Ettlinger, University of Copenhagen, recently detected (unpublished manuscript) benzylglucosinolate in *Batis maritima* L., a species previously reported to contain thioglucosidase (Schraudolf et al., 1971). On the basis of these and other data, Prof. Ettlinger allies the Bataceae with other glucosinolate-containing families (Ettlinger & Kjaer, 1968); furthermore, the isolation of an isothiocyanate from *Codonocarpus cotinifolius* (Desf.) F. Muell. (Bottomley & White, 1950) indicates that the Gyrostemonaceae also belongs with these same families. As noted in the next section, the studies of pollen structure not only support a close relationship of Bataceae to the Gyrostemonaceae but also distinguish these two families from those in the Centrospermae (Goldblatt et al., 1976; Nowicke, 1975).

As a result of discussions with Prof. F. Ehrendorfer (Vienna) and from comments in a recent paper of his (1976), I agree that we must consider the possibility that the betalain families arose from an ancestral taxon which had lost the ability to produce anthocyanins. Such a process would require that the ancestor had lost the one or two enzymatic steps required to convert dihydroflavonols into anthocyanins and subsequently gained the two or three steps needed to form betalamic acid from L-dopa and then condense this aldehyde with various amines and amino acids to produce the red and yellow betalains.

Pollen Morphology in the Centrospermae

Recent investigations (Nowicke, 1975; Skvarla & Nowicke, 1976) of pollen morphology for centrospermous taxa (Table 6) also support a close relationship of the betalain families with the Caryophyllaceae and Molluginaceae in accord with our treatment (Table 4). In her examination of 190 species from 16 families by light and scanning electron microscopy, Nowicke (1975) found three common pollen types, all with a spinulose and tubuliferous/punctate ektexine among the betalain families and the Caryophyllaceae and Molluginaceae. Two additional minor related pollen types were detected in the Nyctaginaceae.

The pollen morphology of other taxa such as Achatocarpaceae, Bataceae, Gyrostemonaceae, Polygonaceae, and Theligonaceae do not support their inclusion in the Centrospermae. Of these, only the Achatocarpaceae would appear to be centrospermous on the basis of having P-III subtype sieve-element plastids; the pigment content of this taxon is not yet known.

Summary

It is our view that all the betalain families and the two anthocyanin families, the Caryophyllaceae and Molluginaceae, are derived from a common "centrospermous" ancestral taxon which evolved the P-III subtype sieve-element plastids now characteristic of all these families. In addition, the ancestor was probably preadapted for C_4 photosynthesis and for a pollen morphology with spinulose and tubiferous/ektexine. The ancestral taxon for the betalain families may have arisen either from a taxon which had anthocyanins, then lost them and later gained betalains, or from a taxon which had not previously contained either type of pigment. In any case, the centrospermous evolutionary complex is now represented by eleven core families which in my opinion are best treated in one order, the Centrospermae or Caryophyllales, which consists of a betalain-suborder, the Chenopodiineae, and an anthocyanin-suborder, the Caryophyllineae (Table 4).

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DEFENSIVE ECOLOGY OF THE CRUCIFERAE[1]

PAUL FEENY[2]

ABSTRACT

The glucosinolates (mustard oil glucosides), present in all crucifer species examined, seem to provide a major line of chemical defense against bacteria, fungi, insects, and mammals. Circumstantial evidence suggests that other classes of secondary compounds, each restricted to one or a few genera, represent a second line of chemical defense.

Survival of wild crucifers depends partly on escape from adapted enemies in time and space. Discovery of crucifers by several enemy species is aided by behavioral responses to glucosinolates or their breakdown products. Allylglucosinolate (sinigrin) in the leaves of *Thlaspi arvense* releases allylthiocyanate instead of the more typical allylisothiocyanate, which is used as a host-finding attractant by several insect species. This change in secondary chemistry may reduce the rate of discovery of *Thlaspi* plants by crucifer-adapted enemies.

The defensive ecology of crucifers seems to typify that of herbaceous plants generally: chemical resistance, in the form of small amounts of toxic compounds, combined with low apparency to enemies which are adapted to the chemical defenses. The importance of the Cruciferae and other families of herbaceous plants as sources of food-plants for man may result in large part from their relatively low concentrations of toxins. The mature foliage of trees, shrubs, and grasses, by contrast, remains poor food for man, just as for other plant enemies.

An important component of the defensive ecology of crucifers and other unapparent plants seems to be chemical diversity in space and time. Closer simulation of this diversity in fields of agricultural crops may reduce the need for synthetic pesticides.

The family Cruciferae comprises approximately 400 genera and 3,000 species, the vast majority of which are herbaceous (Vaughan et al., 1976). The greatest number of species are found in temperate regions of the northern hemisphere, especially in those with a Mediterranean type of climate. The Irano-Turanian region alone contains about 150 genera and 900 species and may well have been the evolutionary cradle of the family, at least in the Old World (Hedge, 1976). The family has colonized a great variety of habitats, including arctic and alpine regions and some of the most climatically inhospitable deserts, though it is poorly represented in the tropics (Hedge, 1976).

The family is the source of several economically important species and varieties, especially the cole crops of the genus *Brassica*. Economic incentives have stimulated extensive research on interactions between crucifers and their associated insects and pathogens. Understanding of the chemical aspects of these interactions has been helped greatly by unusually thorough knowledge of the family's chemistry (see Kjaer, 1976).

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Primary Chemical Defense

The first characteristic line of chemical defense in crucifers is evidently provided by the glucosinolates (mustard oil glucosides, thioglucosides). The occurrence of these compounds, more than 70 of which are known, is restricted almost entirely to the related families Capparaceae, Cruciferae, and Resedaceae. Approximately 300 crucifer species have been examined so far and all contain glucosinolates (Kjaer, 1960, 1976; Ettlinger & Kjaer, 1968). These compounds are hydrolyzed typically to yield volatile isothiocyanates (mustard oils) when plant tissues are damaged; allylglucosinolate (sinigrin), for example, is a major component of plants of the genus *Brassica* and breaks down to allylisothiocyanate:

$$CH_2 = CH - CH_2 - \underset{\diagdown \text{S-Glucose}}{\overset{\text{N-O-SO}_3^- \\ /\!/}{C}} + H_2O \rightarrow CH_2 = CH - CH_2 - NCS + \text{Glucose} + HSO_4^-$$

Allylisothiocyanate, released from allylglucosinolate, is largely responsible for the odor of cooked cabbage (MacLeod, 1976). Hydrolysis of glucosinolates is catalyzed by a group of enzymes (myrosinases) which are stored separately within the plant tissues but which come into contact with their substrates when the plant tissues are bruised or otherwise damaged (Kjaer, 1976; Björkman, 1976). Storage of isothiocyanates in the form of glucosinolates may represent an adaptation to avoid autotoxicity; isothiocyanates are strongly phytotoxic (Hooker et al., 1945; Bell & Muller, 1973).

Glucosinolates or their breakdown products are known to be powerful antibiotics (Virtanen, 1958, 1965) and to inhibit the growth of fungi (Walker et al., 1937) and insects (Brown, 1951; Lichtenstein et al., 1964). The concentration of allylglucosinolate in the foliage of *Brassica nigra* plants in Tompkins County, New York, was found to be about 0.4% of fresh weight, depending somewhat on habitat and leaf age (P. Feeny and L. Contardo, in preparation); at this concentration the compound proved to be toxic to larvae of the black swallowtail butterfly, *Papilio polyxenes*, which naturally feed on umbellifers but occur in the same habitats as many crucifer species in the northeastern United States (Erickson & Feeny, 1974; P. Blau, P. Feeny and L. Contardo, in preparation). Glucosinolates or their hydrolysis products, when ingested in large quantities, are also toxic to mammals; the effect seems to result, at least in part, from the effectiveness of allylisothiocyanate as a tissue irritant (Kingsbury, 1964).

Glucosinolates in crucifers may play a role as allelopathic agents, inhibiting the germination and growth of competing plants. Patches within the annual grasslands of southern California are dominated by *B. nigra*, introduced from Europe. Bell & Muller (1973) showed convincingly that the persistence of these patches from year to year can be attributed to inhibition of the germination and growth of other plants by compounds leached from *B. nigra*. They found that allylisothiocyanate is a potent inhibitor of germination by seeds of several grasses but ruled it out as the allelopathic agent because of its rapid loss of activity in the soil. The unknown toxic compounds are water soluble and are leached from dead *B. nigra* tissues of the previous season's growth by the first fall rains, which

also serve as the stimulus for germination by the seeds of most species (Bell & Muller, 1973). I am not convinced that the authors have completely ruled out the possibility that the allelopathic agent is allylglucosinolate, stored in dead stems during the summer drought period and capable of releasing allylisothiocyanate over a period of time after being leached into the soil.

The available evidence thus suggests that the biological activity of the glucosinolates is broad and supports the contention that predation, disease, and perhaps competition are selective pressures which have contributed to the evolution and diversification of these compounds in the Cruciferae (see also Feeny, 1976).

The Crucifer Fauna

In spite of their content of glucosinolates, crucifers are attacked by an extensive array of insect species, several of which have become major pests of cultivated cruciferous crops. Many of the insect species which attack crucifers are "specialists" which rarely or never attack plants of other families; examples include larvae of the familiar cabbage butterfly, *Pieris rapae*, the cabbage aphid, *Brevicoryne brassicae*, and the cabbage flea beetles *Phyllotreta cruciferae* and *P. striolata* (Root, 1973). Generalist insects which include crucifers among their normal range of host-plants include the cabbage looper, *Trichoplusia ni*, and the green peach aphid, *Myzus persicae*. Crucifers are subject also to attack by an extensive array of fungi and bacteria (Westcott, 1971) and are probably eaten in significant quantities by wild mammals. In view of the deleterious effects of glucosinolates on organisms which do not normally attack crucifers we must presume that the various species making up the typical fauna of natural crucifers are somehow adapted to detoxify glucosinolates or otherwise avoid their harmful effects. The actual mechanisms of detoxification by adapted enemies are not yet known. Larval growth of the cabbage butterfly, *P. rapae*, on a wide range of crucifer species and cultivated varieties was compared recently by Slansky & Feeny (1977). Growth showed no obvious relationship to the varied pattern of glucosinolates present in the test plants but was closely related to the availability of nitrogen in the plant food. Individual glucosinolates vary in their toxicity to nonadapted insects (e.g. Brown, 1951); in crucifer-adapted insects, however, the extent to which tolerance of one glucosinolate confers tolerance of others needs to be examined in more detail.

When concentrations of allylglucosinolate in the leaves of collard plants, *Brassica oleracea*, were artificially increased by culturing to 20 times the typical level, growth of *P. rapae* larvae remained unaffected (P. Blau, P. Feeny and L. Contardo, in preparation). This result suggests that glucosinolates represent "qualitative" or "evolutionary" barriers to nonadapted insects: once overcome by adaptation they have little or no toxic effect in spite of wide variation in concentration (Feeny, 1975, 1976). This is consistent with the finding by van Emden (1972) that relative growth rate of the cabbage aphid, *B. brassicae*, was correlated positively with the "total allylisothiocyanate" content of crucifer test-plants. Glucosinolates stimulate feeding by this crucifer-restricted aphid but they are evidently not toxic to it, at least at concentrations normally encountered in the plants. Dosage-related toxicity of glucosinolates may have greater ecologi-

cal effects on crucifer-adapted bacteria and fungi than it seems to have on insects which specialize on these plants.

The effects of glucosinolates on generalist insects seem to be intermediate between their effects on crucifer-specialists and those on insects which do not naturally attack crucifers. The southern armyworm, *Spodoptera eridania*, and peach aphid, *M. persicae*, naturally attack crucifers as well as plants of many other families. They must therefore be able to tolerate at least low levels of glucosinolates. However, larvae of *S. eridania* have less tolerance for leaves artificially boosted with allylglucosinolate than have larvae of *P. rapae* (P. Blau, P. Feeny and L. Contardo, in preparation) and the relative growth rate of *M. persicae* is correlated negatively with the "total allylisothiocyanate" content of crucifer leaves (van Emden, 1972).

Escape from Adapted Enemies in Space and Time

Such is the ability of adapted enemies to damage and destroy crucifer plants, once they have been discovered, that the survival of crucifers in nature must surely be attributable in large measure to their ephemeral life histories which provide a constantly changing pattern of geographical and phenological distribution. The habitats most favored by crucifers seem to be those in which periods favorable for growth are severely limited by climatic variables such as rainfall (e.g. chaparral, grassland, desert) and temperature (arctic and alpine habitats). Typical crucifers must therefore be capable of rapid growth to maturity and seed-set, and it is perhaps not surprising that so many species have evidently been preadapted to exploit disturbed areas associated with human activities. Short growth season, shifting pattern of geographic distribution, and association with harsh and somewhat unpredictable climatic conditions are all characteristics which are likely to favor escape by plants from their adapted enemies (Janzen, 1970; Rhoades & Cates, 1976; Feeny, 1976).

The importance of escape from adapted insect enemies to the ecology of herbaceous plants was well illustrated by the history of introduced Klamath weed, *Hypericum perforatum*, in California (Huffaker & Kennett, 1959). In 1951 this plant infested more than 2 million acres of range land, covering up to 80% of the ground area in some places. Introduction from Europe of the *Hypericum*-adapted leaf beetles, *Chrysolina quadrigemina* and *C. hyperici*, reduced the plant to less than 1% of its former abundance by 1959. Both plant and beetles continued to persist at low densities, the plant surviving best in shadier habitats where the beetles are less effective (Huffaker & Kennett, 1959). "It would seem that the new low density of *Hypericum perforatum* is maintained at a level at which interplant distance restricts epidemic development of the beetle by limiting its opportunity to discover the isolated specific food plants" (Harper, 1969). While no such dramatic examples are available, it seems, for cruciferous plants, escape from discovery by adapted enemies is likely to be an important component of their defensive ecology also.

Pimentel (1961) and Root (1973) have shown that populations of crucifer-adapted specialists such as *B. brassicae* and *P. cruciferae* reach higher densities on collard plants grown in monoculture patches than on plants grown among di-

verse meadow vegetation. Root (1973) attributed these findings to "resource concentration": herbivores are more likely to find and remain on hosts that are growing in dense or nearly pure stands. An individual collard plant is more "apparent" (i.e., susceptible to discovery) when growing next to other collard plants than when growing among plants of other families (Feeny, 1976). Comparable experiments by Smith (1976) showed that populations of *B. brassicae* and other crucifer-feeding species reached higher levels on Brussels sprout plants grown on weed-free soil than on plants grown among weeds. Trapping experiments showed that weed-free plants were more attractive to colonizing aphids, probably because a background of bare soil presents greater visual contrast than does a background of weeds (Smith, 1976). Diversity of surrounding vegetation may similarly permit wild crucifers in natural habitats to escape or reduce the risk of discovery by searching insects (Feeny, 1976).

Plants of the genus *Dentaria* differ from more typical crucifers in several respects. They are perennial and form patches, often of substantial area, among the ground vegetation of mature deciduous forests. The plants leaf out very early in the spring and approach senescence by the time the forest canopy has leafed out. Plants of *D. diphylla* were damaged heavily, after transplanting into open field habitats, by the typical open-habitat crucifer flea beetles *P. cruciferae* and *P. striolata* (Hicks & Tahvanainen, 1974) and *Dentaria* leaves supported better growth of *P. rapae* larvae than did those of any other crucifer tested (Slansky & Feeny, 1977). Though subject to their own specialized enemies, such as the butterfly *Pieris virginiensis* and the flea beetle *Phyllotreta bipustulata*, *Dentaria* species have probably benefited by their escape, in evolutionary time, into a habitat which is atypical of crucifers and thus not frequented by many of the typical crucifer-adapted enemies.

Plant-Finding Adaptations

Many crucifer-adapted insects have evolved behavioral responses to glucosinolates or their breakdown products, thus permitting them to find their foodplants more easily and to discriminate them from other vegetation. An early example of such behavior was described by Verschaffelt (1911) who found that larvae of *P. brassicae* and *P. rapae* can be stimulated to feed on normally rejected plants by treating the plants with solutions of allylglucosinolate. A recent review by Schoonhoven (1972) lists a dozen insect species which are known to make use of these compounds as behavioral cues. There is even a crucifer-adapted fungus, *Plasmodiophora brassicae*, the spores of which are stimulated to germinate by the presence of allylisothiocyanate (Hooker et al., 1945). Behavioral responses to glucosinolates or isothiocyanates by individuals of any one insect species usually depend on concentration and may also vary from one compound to another (e.g., Thorsteinson, 1953; Hicks, 1974; Finch & Skinner, 1974).

The crucifer-feeding flea beetles, *Phyllotreta cruciferae* and *P. striolata*, are strongly attracted to traps containing solutions of allylisothiocyanate (Feeny et al., 1970) and can also be induced to eat bean leaves, which they normally reject, when these have been cultured in solutions of allyglucosinolate (Hicks,

1974). We have found recently that addition of vials containing solutions of allylglucosinolate in mineral oil to 3-plant islands of *Brassica nigra*, planted among diverse vegetation, greatly accelerated the rate of discovery of the plants by these flea beetles (P. Feeny, J. Gaasch and L. Contardo, in preparation). This finding not only confirms the effectiveness of allylisothiocyanate as a host-finding attractant but also shows that leakage of such compounds, even in small amounts, can be a liability to *B. nigra* plants since it increases their apparency to adapted enemies.

SECONDARY DEFENSE IN CRUCIFERS

Many crucifers are known to contain other secondary compounds in addition to glucosinolates. The genera *Erysimum* and *Cheiranthus*, for example, contain cardenolides, the genus *Iberis* contains cucurbitacins, and plants of the genera *Lunaria* and *Capsella* contain alkaloids (Gheorghiu et al., 1959; Hegnauer, 1964). The genera *Lepidium* and *Thlaspi* contain atypical enzymes which break down glucosinolates not to the typical isothiocyanates but to their corresponding geometrical isomers, the thiocyanates (Gmelin & Virtanen, 1959).

Many of these plants are avoided by crucifer-adapted insects or, if fed upon, support unusually poor growth. Larvae of *P. rapae*, for instance, grow poorly on *Thlaspi arvense*, *Lepidium virginicum*, and *Lunaria annua* (Slansky & Feeny, 1977); they will refuse to eat leaves of *Erysimum cheiranthoides* and *Capsella bursa-pastoris* (A. M. Shapiro, personal communication). Verschaffelt (1911) found that *C. bursa-pastoris* was attacked only very slightly by larvae of *P. rapae* and *P. brassicae*; *E. perofskianum* was also less preferred by these larvae relative to most other crucifers offered to them. Plants of *E. cheiranthoides*, *C. bursa-pastoris*, and *Iberis amara* are not eaten by *P. cruciferae* flea beetles (Feeny et al., 1970). Chew (1975) found that larvae of *Pieris napi macdunnoughii* in Colorado refused to eat *Erysimum asperum*. Larvae of *P. napi macdunnoughii* grew normally on *Thlaspi montanum*, a native plant in Colorado, but they and larvae of *P. occidentalis* died after eating *T. arvense*, an introduced species. The unusual resistance of plants of these genera to typical crucifer enemies may result from their content of atypical secondary compounds (see Verschaffelt, 1911). Allylthiocyanate, for example, is known to be toxic to insects (Brown, 1951). Such compounds could have been evolved as a "second line of defense" in response to enemies which have evolved mechanisms for tolerating glucosinolates and their typical hydrolysis products. Diversification of secondary chemistry, in other words, may permit escape from certain enemies in evolutionary time, at least until further counteradaptations are evolved by the associated insects or other enemies.

In addition to their possible toxic or growth-inhibitory effects, unusual secondary compounds may further benefit a plant species by reducing apparency to adapted enemies. Hydrolysis of allylglucosinolate in leaves of *Thlaspi arvense* yields allylthiocyanate instead of the more typical allylisothiocyanate (Gmelin & Virtanen, 1959; P. Feeny and L. Contardo, in preparation). Three-plant islands of *T. arvense* were colonized by *Phyllotreta* flea beetles at a considerably slower rate than were nearby islands of *Brassica nigra*, perhaps because allyliso-

thiocyanate is an attractant to the beetles whereas allylthiocyanate is not. Colonization of *T. arvense* islands was accelerated by addition of vials containing solutions of allylisothiocyanate (P. Feeny, J. Gaasch and L. Contardo, in preparation).

Crucifers may derive additional protection from adapted enemies as a result of association with plants of different chemistry. Tahvanainen & Root (1972) have found that odors from tomato, *Lycopersicon lycopersicum* (=*esculentum*), and ragweed, *Ambrosia artemisifolia*, plants interfered with the ability of *P. cruciferae* flea beetles to find crucifer host-plants. The reduction of plant apparency to enemies by neighboring plants of different species is an important component of "associational resistance" (Tahvanainen & Root, 1972)—a phenomenon frequently exploited by organic gardeners.

Chemical Defense and the Human Diet

The defensive ecology of crucifers seems to typify that of many ephemeral herbaceous plants—plants which rely to a great extent on being hard to find (unapparent) in natural habitats. Such plants seem to contain rather low concentrations of effective toxins. They probably benefit from a diversity of chemical defense in any one species and from association with other plants of different chemistry (Rhoades & Cates, 1976; Feeny, 1976). Their defenses clearly differ from those of the mature foliage of more persistent plants such as shrubs and trees. Such plants are bound to be found by enemies and must correspondingly be well defended; they often contain large amounts of general growth-inhibitory compounds, like tannins, resins and silica, which are resistant to simple counter-adaptation. The foliage of apparent plants is usually tough and deficient in nutrients and water when compared with that of most herbaceous plants (Rhoades & Cates, 1976; Feeny, 1976).

These differences in the defensive ecology of plants, depending upon their apparency to enemies, seem to be reflected in human food preferences. One hundred students in the general ecology course at Cornell University were asked to list as many species of human food-plants as they could think of in 15 minutes. Their total of 108 species, excluding plants used primarily as spices and drugs, was then tabulated by plant growth form and by what part of the plant is eaten (Fig. 1 and Appendix). Though undoubtedly a biased view of more general patterns of plant consumption by man, this survey revealed some interesting and suggestive trends.

Most of the species listed are harvested only for their fruits or seeds, and of these species most are trees (Fig. 1). The production of fleshy fruits is probably an adaptation for seed dispersal by vertebrate animals, including our primate ancestors. Ripe fruits are adapted to be attractive to animals by their size, color, and taste; fruit-eating behavior by the animals is probably reinforced by the fact that fruits contain not only energy-rich carbohydrates and fats but also vitamins and mineral ions which are vital for the survival of many vertebrate animals and not readily available from other natural sources (see McKey, 1975). One can even speculate that our "sweet tooth," now a conspicuous liability in times of readily available sugar, represents a physiological adaptation which

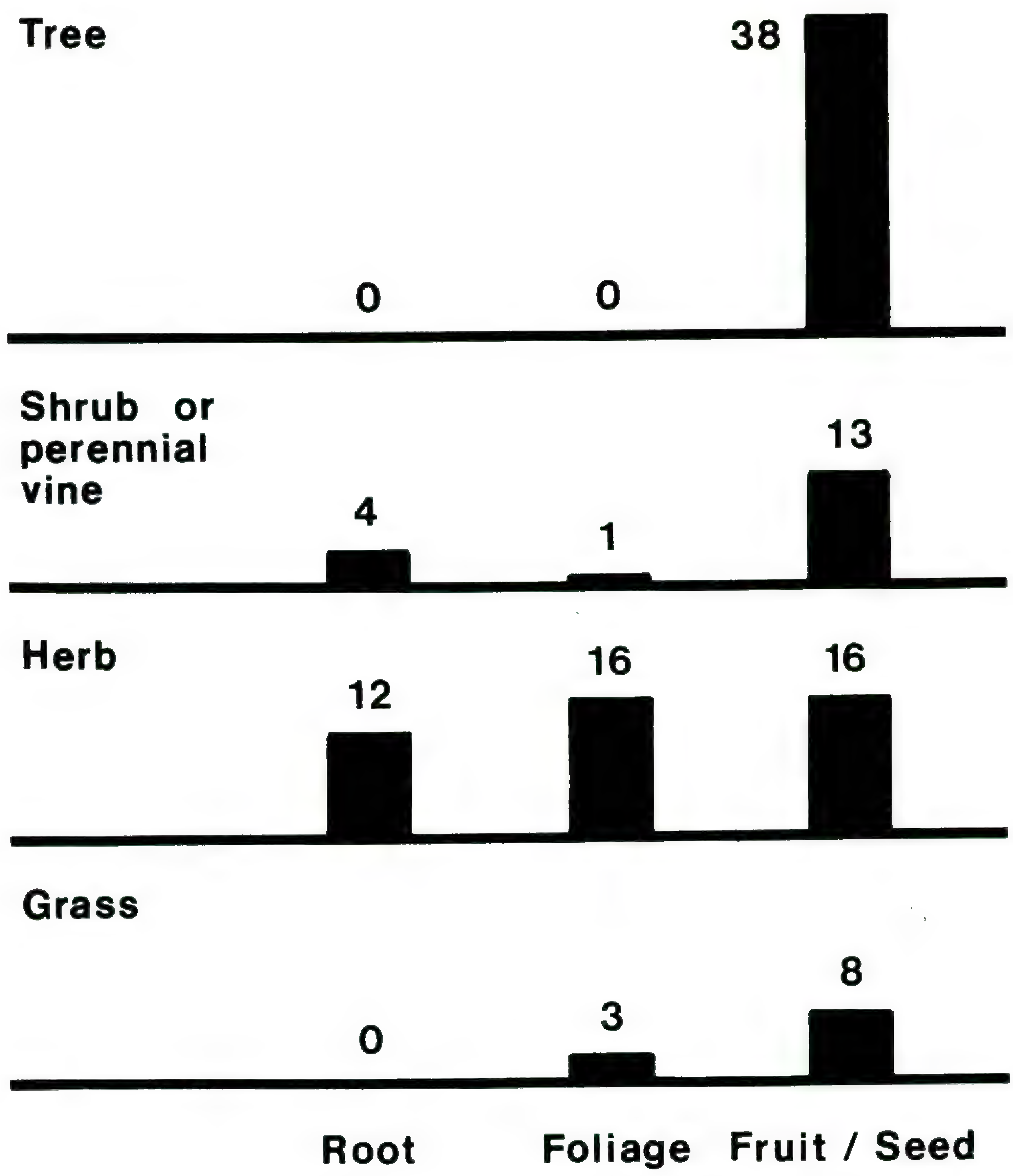

FIGURE 1. Distribution of 108 species of human food-plants according to plant growth form and part of plant eaten. Figures indicate number of food-plants listed in each category (3 species listed twice). See Appendix for details.

stimulated our ancestors to seek out fruits with their high nutrient value (see Yudkin, 1969).

A second striking pattern reflected in this survey is that plants whose roots or leaves form part of the human diet are almost all herbs (Fig. 1). These are the plants, including the ancestors of our cruciferous vegetables, which tend to be ephemeral and unapparent in nature. The origins of cultivated plants from herbaceous species were probably due to the concentrated food value of the roots or tubers of many of these species and to the unique preadaptations of

"weedy" plants to thrive in the disturbed habitats associated with human habitation (Hawkes, 1969). Preferential consumption of herbaceous species may also reflect the presence in trees and shrubs of extensive chemical and physical defenses, evolved by trees and shrubs because they are relatively apparent to natural enemies. Many of the drugs and spices used by man come from the foliage and roots of trees and shrubs, though they are rarely consumed in large quantities. By contrast we are presumably able to tolerate the comparatively low concentrations of defensive compounds in crucifers and other herbaceous plants both because of the detoxication enzymes concentrated in the vertebrate liver (Freeland & Janzen, 1974) and also, since the cultural evolution of the use of fire, because we further detoxify or remove many of these compounds by cooking (Yudkin, 1969; Leopold & Ardrey, 1972). Only because they contain relatively small concentrations of toxins can we consume such plants in large quantities.

Apparency and Agriculture

The effectiveness of natural plant defenses is reduced by present agricultural methods. When they are planted in monocultures, crop plants become more apparent to natural enemies than are their ancestors in nature, yet they possess chemical and physical defenses inappropriate for survival as apparent plants. This is a major reason that substantial quantities of synthetic pesticides are often required to prevent widespread devastation of crops.

It would undoubtedly be possible to modify crop varieties and agricultural methods so as to mimic the defensive ecology of wild ancestral plants more closely. Levels of natural defensive compounds could be maintained or restored by selective plant breeding and emphasis placed on diversity of defense within any particular crop species. Plant apparency could be reduced by such traditional techniques as crop rotation and interplanting of different crops or chemical varieties of any one crop. Apparency could be reduced further by eliminating or modifying those plant chemicals which the more important plant enemies use as behavioral attractants or feeding stimulants.

Strategies to improve and diversify chemical resistance would be more effective if they were coordinated with strategies to reduce plant apparency. Just as the evolution of resistance to a particular pesticide by an insect population may result from extensive and repeated exposure to that compound, so also the fewer the insects which find a particular plant variety, the less likely they are to evolve methods of tolerating the plant's chemical defenses (Southwood, 1973).

A key component of the defensive ecology of crucifers and other unapparent plants seems to be chemical diversity in space and time (Rhoades & Cates, 1976; Futuyma, 1976; Feeny, 1976). The more closely we can simulate this diversity in our fields of vegetable crops, the less dependent are we likely to become on the use of synthetic pesticides to achieve a given level of agricultural production.

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APPENDIX

Species of human food-plants listed by 100 students in the general ecology course (Bio. Sci. 360, Fall 1976) at Cornell University, and categorized as a function of: (1) Growth form of plant and (2) Part of plant eaten. Bulbs and tubers are included with roots; shoots, stems and flower parts are included with foliage. Three species (*Vitis vinifera*, *Beta vulgaris*, and *Brassica rapa*) are listed twice. an. = annual, bien. = biennial, per. = perennial.

A. TREES			
(i) *Root*: No species listed.			
(ii) *Foliage*: No species listed.			
(iii) *Fruit*:			
Mango	*Mangifera indica*	tree	Anacardiaceae
Pawpaw	*Asimina triloba*	small tree	Annonaceae
Papaya	*Carica papaya*	small tree	Caricaceae
Japanese persimmon	*Diospyros kaki*	tree	Ebenaceae
Avocado	*Persea americana*	tree	Lauraceae
Fig	*Ficus carica*	tree	Moraceae
Breadfruit	*Artocarpus altilis*	tree	Moraceae
Banana, plantain	*Musa acuminata* and	tall per. herb	Musaceae
	Musa ×paradisiaca	tall per. herb	Musaceae
Common guava	*Psidium guajava*	small tree	Myrtaceae
Olive	*Olea europaea*	tree	Oleaceae
Date	*Phoenix dactylifera*	tall palm	Palmaceae
Pomegranate	*Punica granatum*	small tree	Punicaceae
Quince	*Cydonia oblonga*	small tree	Rosaceae
Apple	*Malus pumila*	tree	Rosaceae
Pear	*Pyrus communis*	tree	Rosaceae
Apricot	*Prunus armenica*	small tree	Rosaceae
Sweet cherry	*Prunus avium*	tree	Rosaceae
Plum	*Prunus domestica*	small tree	Rosaceae
Peach, nectarine	*Prunus persica*	small tree	Rosaceae
Sweet orange	*Citrus sinensis*	tree	Rutaceae
Grapefruit	*Citrus ×paradisi*	small tree	Rutaceae
Nagami kumquat	*Fortunella margarita*	small tree	Rutaceae
(iv) *Seed*:			
Cashew	*Anacardium occidentale*	tree	Anacardiaceae
Pistachio	*Pistacia vera*	small tree	Anacardiaceae
European filbert/hazelnut	*Corylus avellana*	small tree	Corylaceae
American filbert/hazelnut	*Corylus americana*	small tree	Corylaceae
European chestnut	*Castanea sativa*	tree	Fagaceae
Beech	*Fagus grandifolia*	tree	Fagaceae
Pecan	*Carya illinoensis*	tree	Juglandaceae
Hickory	*Carya ovata* and	tree	Juglandaceae
	Carya laciniosa	tree	Juglandaceae
Butternut	*Juglans cinerea*	tree	Juglandaceae
English walnut	*Juglans regia*	tree	Juglandaceae
Brazil nut	*Bertholletia excelsa*	tree	Lecythidaceae
Coconut	*Cocos nucifera*	tall palm	Palmaceae
Piñon	*Pinus cembroides*	tree	Pinaceae
Almond	*Prunus dulcis*	small tree	Rosaceae
B. SHRUBS AND PERENNIAL VINES			
(i) *Root*:			
Sweet potato (tuber)	*Ipomoea batatas*	per. vine	Convolvulaceae
Yam	*Dioscorea* spp.	per. vine	Dioscoreaceae
Cassava/manioc	*Manihot esculenta*	shrub	Euphorbiaceae
Ground nut (tuber)	*Apios americana*	per. vine	Leguminosae
(ii) *Foliage*:			
European grape	*Vitis vinifera*	per. vine	Vitaceae

APPENDIX. (continued)

(iii) *Fruit*:			
American elder	*Sambucus canadensis*	shrub	Caprifoliaceae
Huckleberry	*Gaylussacia* spp.	shrub	Ericaceae
Cranberry	*Vaccinium macrocarpon*	shrub	Ericaceae
Blueberry	*Vaccinium* spp.	shrub	Ericaceae
Passion fruit/purple granadilla	*Passiflora edulis*	per. vine	Passifloraceae
Red raspberry	*Rubus idaeus*	shrub	Rosaceae
Black raspberry	*Rubus occidentalis*	shrub	Rosaceae
Loganberry, boysenberry	*Rubus ursinus*	shrub	Rosaceae
Rose hip	*Rosa villosa*	shrub	Rosaceae
American gooseberry	*Ribes hirtellum*	shrub	Saxifragaceae
Red currant	*Ribes sativum*	shrub	Saxifragaceae
Fox grape	*Vitis labrusca*	per. vine	Vitaceae
European grape	*Vitis vinifera*	per. vine	Vitaceae
(iv) *Seed*: No species listed.			
C. HERBACEOUS PLANTS			
(i) *Root*:			
Onion (bulb)	*Allium cepa*	per.	Amaryllidaceae
Beet, sugar beet	*Beta vulgaris*	an./bien.	Chenopodiaceae
Rutabaga	*Brassica napus*	an./bien.	Cruciferae
Turnip	*Brassica rapa*	an./bien.	Cruciferae
Radish	*Raphanus sativus*	an./bien.	Cruciferae
Burdock	*Arctium lappa*	per.	Compositae
Jerusalem artichoke (tuber)	*Helianthus tuberosus*	per.	Compositae
Camass (bulb)	*Camassia quamash*	per.	Liliaceae
Potato (tuber)	*Solanum tuberosum*	per.	Solanaceae
Cattail	*Typha* spp.	per.	Typhaceae
Carrot	*Daucus carota*	an./bien.	Umbelliferae
Parsnip	*Pastinaca sativa*	bien.	Umbelliferae
(ii) *Foliage*:			
Leek	*Allium ampeloprasum*	bien.	Amaryllidaceae
Comfrey	*Symphytum officinale*	per.	Boraginaceae
Beet	*Beta vulgaris*	an./bien.	Chenopodiaceae
Spinach	*Spinacea oleracea*	an./bien.	Chenopodiaceae
Cabbage, kale, etc.	*Brassica oleracea*	an./bien.	Cruciferae
Chinese cabbage	*Brassica rapa*	an./bien.	Cruciferae
Water cress	*Nasturtium officinale*	per.	Cruciferae
Endive	*Cichorium endivia*	an./bien.	Compositae
Chicory	*Cichorium intybus*	per.	Compositae
Artichoke (flower bud and scales)	*Cynara scolymus*	per.	Compositae
Lettuce	*Lactuca sativa*	an./bien.	Compositae
Dandelion	*Taraxacum officinale*	per.	Compositae
Asparagus (young stem)	*Asparagus officinalis*	per.	Liliaceae
Rhubarb (leaf stalk)	*Rheum rhabarbarum*	per.	Polygonaceae
Celery (leaf stalk)	*Apium graveolens*	bien.	Umbelliferae
Fennel (leaf stalk)	*Foeniculum vulgare*	an./per.	Umbelliferae
(iii) *Fruit*:			
Pineapple	*Ananas comosus*	per.	Bromeliaceae
Sunflower	*Helianthus annuus*	an.	Compositae
Watermelon	*Citrullus lanatus*	an. vine	Cucurbitaceae
Melon	*Cucumis melo*	an. vine	Cucurbitaceae
Cucumber	*Cucumis sativus*	an. vine	Cucurbitaceae
Squash, pumpkin, zucchini	*Cucurbita* spp.	an. vine	Cucurbitaceae
Strawberry	*Fragaria* ×*ananassa*	per.	Rosaceae
Green pepper, chili	*Capsicum annuum*	an./per.	Solanaceae

APPENDIX. (continued)

Tomato	*Lycopersicon lycopersicum*	an./per.	Solanaceae
Eggplant	*Solanum melongena*	an./per.	Solanaceae
(iv) *Seed*:			
Peanut	*Arachis hypogaea*	an.	Leguminosae
Soybean	*Glycine max*	an.	Leguminosae
Lentil	*Lens culinaris*	an.	Leguminosae
Lima bean	*Phaseolus limensis*	an./per.	Leguminosae
Kidney bean	*Phaseolus vulgaris*	an.	Leguminosae
Garden pea	*Pisum sativum*	an. vine	Leguminosae
D. GRASSES			
(i) *Root*: No species listed.			
(ii) *Foliage*:			
Bamboo (young shoots)	*Phyllostachys* spp. and	per.	Gramineae
	Bambusa spp.	per.	Gramineae
Sugar cane (stems)	*Saccharum officinarum*	per.	Gramineae
(iii) *Fruit*: No species listed.			
(iv) *Seed*:			
Oat	*Avena sativa*	an.	Gramineae
Barley	*Hordeum vulgare*	an.	Gramineae
Rice	*Oryza sativa*	an.	Gramineae
Broomcorn/millet	*Panicum miliaceum*	an.	Gramineae
Rye	*Secale cereale*	an.	Gramineae
Sorghum	*Sorghum bicolor*	an.	Gramineae
Common wheat	*Triticum aestivum*	an.	Gramineae
Corn	*Zea mays*	an.	Gramineae

CHEMOSYSTEMATICS AND ITS EFFECT UPON THE TRADITIONALIST[1]

B. L. TURNER[2]

What is a traditionalist, taxonomically speaking? I suppose a traditionalist might best be defined as a taxonomist trained as a pheneticist, practicing his trade as a pheneticist, and constructing his classification using primarily phenetic data. By this definition I am a traditionalist and consequently can claim to answer, *for myself*, the effect of chemosystematics upon my own traditional attitudes and outlooks. And this has been profound.

I say profound *not* because this new field has solved any large number of critical problems in plant taxonomy, but because where it has been used with skill and judgement, it has proved much more effective than phenetics in solving the particular problems concerned. Indeed, without chemical data many of the more intractable problems having to do with familial relationships among flowering plants generally are likely to remain unresolved: there are simply too many cooks and nearly all with varying tastes. Even if they all see the same phenetic substances in the phyletic cabinet, they nonetheless are prone to come up with different combinations of this or that ingredient (selected characters), with varying amounts (intuitive weighting), to say nothing of the condition (basic I.Q.) or temperature (zealousness) of the oven (i.e., brain).

I suspect that most traditionalists, even some of the best, do not like to be reminded that their approach is fraught with such variables, or that data derived from some other discipline might prove superior to those from their own.

As an example, when the late Dr. Alston and I first showed the utility of paper chromatography for resolving problems of natural hybridization in *Baptisia*, an eminent, not so classical, plant systematist suggested that our documentation of complex hybridization in this genus could have been accomplished with equal clarity using selected morphological characters arranged upon Anderson-type scatter diagrams. Needless to say this intellectual guffaw was issued by the late Edgar Anderson, and the ironic part of all this is that Anderson himself was the first to collect and call attention to the existence of hybrid swarms among this group of plants (Anderson, in Larisey, 1940b), but he failed to perceive its complexity, in spite of the fact that he collected his hybrid populations of *Baptisia* in a region where the potential for trihybridization is not infrequent (Alston & Turner, 1963). In fact, I seriously doubt that Anderson, *or any traditional* systematist, including myself, would have been able to recognize, much less intuit, trihybridization within this group, to say nothing of its documentation with reasonable certainty using morphological characters.

Trihybridization, of course, is rather the exception in nature: most species tend to comingle two at a time at any one site. But even then, lacking *in situ* clues (for example, two parental taxa occurring together with their putative

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hybrids, as happens with *Baptisia* upon occasion), two-way hybrids may be difficult to detect, especially where these are quite distinct and relatively widely distributed. Hence we find the southeastern taxon, *Baptisia serenae* Curtis, being recognized as a good species for over 125 years by a wide range of workers, including such an outstanding traditional worker as Wilbur (1963). It is, however, an F_1 hybrid of *B. tinctoria* (L.) Vent. × *B. alba* (L.) Vent. A more remarkable F_1 hybrid, also long-recognized as a good species by nearly all traditionalists, including the only recent monographer of the genus (Larisey, 1940a) is *B. microphylla* Nutt., this being the relatively rare hybrid between *B. perfoliata* (L.) R. Br. and *B. lanceolata* (Walt.) Ell. While it is perhaps likely that these very distinct F_1 hybrids would have been detected if they were found growing with their putative parents, reasonable verification, short of long and laborious crossing experiments, would be difficult. If, however, their flavonoid profiles were sufficiently different, putative F_1 hybrids might be readily confirmed, even from hybrids mounted on herbarium sheets up to 100 years old.

Speaking of the superiority of micromolecular data for the resolution of systematic problems, the most telling example of its efficacy is that involving the detection of allopatric introgression. Edgar Anderson (1949) in an Epilogue to his brilliantly conceived text, *Introgressive Hybridization*, made the following statement:

> How important is introgressive hybridization? I do not know. One point seems fairly certain: its importance is paradoxical. The more imperceptible introgression becomes, the greater is its biological significance. It may be of the greatest fundamental importance when by our present crude methods we can do no more than to demonstrate its existence. When, on the other hand, it leads to bizarre hybrid swarms, apparent even to the casual passer-by, it may be of little general significance . . . . Only by the exact comparisons of populations can we demonstrate the phenomenon . . . . The wider spread of a few genes (if it exists) might well be imperceptible even from a study of population averages, but it would be of tremendous biological import . . . . Hence our paradox. Introgression is of the greater biological significance, the less is the impact apparent to casual inspection.

In other words, in well-differentiated, sympatric species such as *Baptisia* where natural hybridization can be easily recognized and readily documented, its biological impact on evolutionary processes is negligible. But in allopatric situations where hybridization is very difficult to detect it is likely to be of the greatest biological significance.

In spite of these reflections from the foremost proponent of introgressive hybridization, few, if any, well-documented studies have been forthcoming on allopatric introgression. In fact, *the best documented* case in the literature for allopatric introgression is reportedly that involving *Juniperus virginiana* L. and *J. ashei* Buchh. (Anderson, 1953; Davis & Heywood, 1963). However, in a number of detailed studies, centered at The University of Texas (using 60 to 80 chemical characters as detected by gas chromatography as well as morphological characters which distinguish between the taxa), the existence of F_1 hybrids or their immediate derivatives could not be detected, even at sites where large populations of both species grew intermixed, and in *no instance* could the existence of introgression be inferred from the data accumulated (Flake, von Rudloff & Turner, 1969; Adams & Turner, 1970; Flake, von Rudloff & Turner, 1973). In short, what was taken to be a very well-documented case study of allopatric

introgression turned out to be a situation in which clinal intergradation in habital features over a broad region occurred such that, *superficially*, hybridization and introgression might be inferred.

In hindsight, it now seems rather reasonable to have viewed the case study of introgression between *J. virginiana* and *J. ashei* with considerable doubt, for the two species are readily distinguished by a number of morphological features and are placed in different species—groups (sections) of the genus, and the character used for such taxonomic segregation (cilia along the leaf margins) does not, to our knowledge, segregate in putative hybrid swarms (i.e., the two species can always be recognized by this feature, and others, as attested to by the repeated correlation of this character with a plethora of chemical characters); other experienced field workers such as D. S. Correll (pers. comm.) have also had no difficulty in placing the plants concerned in one taxon or the other. In fact, as already indicated, the morphological variation found in *J. virginiana* is clinal, i.e., the species has formed or is in the process of forming regional races as a result of adaptational mechanisms arising out of its own gene pool, this being unrelated to the possible influx of genes from the largely allopatric *J. ashei*. Our work has substantiated fully these suppositions (Flake & Turner, 1973). Again, it is ironic that Hall, who was Anderson's student, should have documented introgressive hybridization where this was not occurring. We attribute this to the plasticity of the morphological characters selected for its detection. It was the absoluteness of the chemical data themselves which permitted resolution of the problem.

What we were left with then was no well-documented case study of allopatric introgression of a regional nature. Fortunately, however, there has been a recent, carefully conceived, populational study of *J. virginiana* and *J. scopulorum* Sarg. in the Missouri River Basin of the north central United States by Van Haverbeke (1968a) which appears to be a situation involving allopatric introgression of the type Anderson felt to be so important in evolutionary processes. The study seems to be unusually well documented. Van Haverbeke made very accurate records of the populational sites, including precise data on ten individually marked trees which were selected for study at each site. These included photographs and detailed field notes. In short, the *J. virginiana-J. scopulorum* complex appeared to provide an ideal case study of allopatric introgression using the chemonumerical methods that proved so effective in *disproving* the occurrence of this phenomenon in the *J. ashei-J. virginiana* "complex."

Van Haverbeke (1968a), through his study of these two taxa in the Missouri River Basin, has stated that:

> The entire *Juniperus* population within the Basin is apparently of hybrid derivation with neither of the extreme parental types being found. There is a trend of increasing hybrid index values (also percentage germ plasm values) from southeast to northwest over the Basin from the reported range of *J. virginiana* to and into the reported range of *J. scopulorum*. This condition may be the result of bilateral introgression between the two species. There was, however, a strong tendency toward bimodality within the population as demonstrated by the presence of two distributions in each of the three hybrid indices. This indicated the presence of two different species—*J. scopulorum* and *J. virginiana*.

While Van Haverbeke (1968b) admits his data might be interpreted as

constituting evidence for introgression he, nevertheless, suggests, indeed champions, an alternate hypothesis:

> As an alternative interpretation, it would seem that because of the greater diversity of the junipers in western North America, that *J. virginiana* was at some time derived from this area. It seems possible that with the inherent variability in the germ plasm ancestral to both *J. scopulorum* and *J. virginiana*, that propagules could flourish in sites toward the east. This could have initiated an eastward migration-propagule—which through mutation and selection eventually became what we now recognize as *J. virginiana*."

It should be noted that this latter evolutionary model is in direct conflict with that proposed by us (Flake, von Rudloff & Turner, 1969, 1973) in which we suggest that the Appalachian Region is the ancestral center for the origin of *J. virginiana* and its various races. Hence, the question of introgression between *J. virginiana* and *J. scopulorum* is left open by Van Haverbeke's study.

Initial investigation of the terpenes of *Juniperus scopulorum*, unlike that of *J. ashei*, showed that its volatile components were essentially those of *J. virginiana*, differing only in their quantitative expression. Subsequent populational analysis of the type employed in the *J. ashei-J. virginiana* studies showed that regional intergradation of the chemical characters occurred across the Missouri River Basin, much as found by Fassett (1944) and Van Haverbeke (1968a) for morphological features.

Three models might be proposed to account for the variation found in this region:

1. ANCESTRAL GENE POOL—*Juniperus scopulorum* and *J. virginiana* may have arisen from ancestral populations largely endemic to the Missouri River Basin. Subsequent evolutionary divergence to the west and east, respectively, might have occurred, leaving a residuum of genes common to each in the area concerned.

2. ALLOPATRIC INTROGRESSION—The variability is due to extensive gene flow from *J. scopulorum* into *J. virginiana* as a result of hybridization and backcrossing in peripheral regions of contact and areas of sympatry.

3. MIGRATORY TAILINGS—The River Basin was an ancestral migratory route through which *J. scopulorum*-like populations passed on their way to becoming what is now known in the eastern United States as *J. virginiana*. In Van Haverbeke's words (1968b), "Thus, rather than being considered as an introgressive series, this juniper population [those of the Missouri River Basin] can alternatively be interpreted as a divergent evolutionary series which has not yet completely separated."

It should be emphasized that in the investigation by Van Haverbeke about 40 morphological characters were selected for measurement and numerical analysis. These were obtained from some 700 trees from 72 sites scattered throughout the River Basin area. In spite of this excellently conceived, carefully documented, laborious study, the investigator was unable to decide, unequivocally, between models 2 and 3; in fact, he believed that his data best fit the migratory tailings model. (Model 1 was not tested, presumably because of its implausibility, considering the biogeographic history of the Basin region.)

Our own study (Flake, Urbatsch & Turner, 1978) also involved about 40 characters, all chemical. These were obtained from some 200 trees from 10 sites

systematically selected at about 150-mile intervals in a southeast-northwest transect across the Basin. In spite of the fewer populations sampled and the smaller overall sample size, we conclude our data overwhelmingly suggest that the variable River Basin populations are the result of allopatric introgression, primarily in the direction of *J. virginiana*, much as Van Haverbeke thought might be the case, but the morphological characters which he used were not sufficiently indicative to prove decisive.

Macromolecular Approaches

If I were interested in obtaining the most meaningful arrangement of present-day angiosperm families, *phylogenetically speaking*, I would rather have available to me the primary structure (amino acid sequence) of ten *metabolically important* enzymes (such as cytochrome *c*) of all of the taxa which comprise these groups than have a detailed listing of all of the exomorphic features which characterize the groups (Turner, 1969).

The nature and proper taxonomic position of the hypothetical past organisms that represent the branch points in the scheme cannot be determined solely from the phylogenetic relationships of modern species as deciphered from the amino acid sequences (Cronquist, 1976).

Protein sequencing and other molecular methods may, in fact, become in the near future the most powerful tools for the study of phlogeny (Ayala, 1976).

The amino acid sequence trees are obviously more compatible with some possible phylogenetic interpretations than others, or there would be no point in making them at all. If we assumed that they were in all respects correct insofar as they go, they would place certain limits on the general phylogenetic trees that could be seriously considered (Cronquist, 1976).

Though this be madness, yet there is method in't (Shakespeare, Hamlet, Scene II, Act 2).

. . . fossil evidence is highly in accord with an overwhelming mass of evidence from comparative morphology of living species that the Magnoliidae are the most primitive (i.e., least modified) group of living angiosperms . . . (Cronquist, 1976).

. . . the molecular tree indicates that present-day families represent relic groups which have for the most part had a long separate evolutionary history. They do not support the suggestion implicit in, for example, Cronquist's scheme . . . that the Magnoliidae gave rise to the Caryophyllidae on the one hand, and to the Rosidae on the other, the latter, in turn, giving rise to the Asteridae (Boulter, 1973).

Something is rotten in the state of Denmark (Shakespeare, Hamlet, Scene IV, Act 1).

With relatively few exceptions, the traditionalist might yawn at the seemingly trivial impact of micromolecular data upon his various systematic models. But he has not yet been able to treat with indifference the likely impact of macromolecular data upon his most treasured erection, the "Tree" to plant families. As unrecognizable as this tree might be to the various workers concerned, any reinsertion of branches or elevation of roots, using such chemical data, is met with alarming cries from this or that proponent. I refer specifically to the recent paper by Cronquist (1976) entitled, "The Taxonomic Significance of the Structure of Plant Proteins: A Classical Taxonomist's View." This is a 27-page rambling review covering the whole field of comparative enzymology, the gist of which is, because these data do not or have not supported my particular views, there must be something wrong with the approach.

The approach is the same as that which has been applied to animals successfully, namely, the use of amino acids among the homologous proteins in different

organisms as an indicator of time of branching. And, strangely enough, he accepts, in principle, the use of cytochrome *c* as a reasonable, but often unsteady, clock for animals, yet rejects this as valid for plants. I quote:

> Given the difference in evolutionary pattern between plants and animals, it should not be surprising if the animal physiological system places stronger constraints on the acceptance of amino acid substitutions in cytochrome *c* than does the plant physiological system. It would be entirely in harmony with the other differences in plant and animal evolution if the same kinds of changes could be accepted by very different sorts of plants and if back mutations were not notably counter-selective.

Cronquist focuses his attack largely upon the data from Boulter's laboratory in Durham, England, which is the only group to sequence any significant number of plant proteins, namely plastocyanin and cytochrome *c*. Amino acid sequences from the latter, in particular, suggest that the familial tree is quite different from the one proposed by Cronquist (and, of course, that of Takhtajan, the two being quite similar). This is disturbing: everyone should accept that the Magnoliidae among the angiosperms is primitive to everything else. He does not like the Caryophyllidae coming off as a first branch on the cytochrome *c* familial tree. He does not like to think of the morphologically highly advanced Compositae represented as a very old isolated branch; everyone should know that it is recent, going back to the Miocene-Oligocene boundary (in spite of the fact that he acknowledges in footnote form that very recently published and unpublished pollen fossil data might push the family back to the Paleocene, if not earlier).

To me, it is remarkable that a traditionalist of his stature, fully aware of the ubiquity of this macromolecule among organisms generally and cognizant of its crucial role in the metabolic pathway of both plants and animals, should attribute the discrepancies to poor or erratic functioning of this kind of clock, rather than to the morphological data, which, after all, has no face, no dial, no nothing to suggest *the time* of branching of this or that phyletic line.

Cronquist (1976: 5), while accepting the general premise that the cytochrome *c* clock works for animals, nevertheless makes great gloat over the fact that the amino acid sequence of rattlesnake cytochrome *c* is out-of-line with the position of that organism in the phyletic tree. There follows a typical Cronquistian quote, "If the reported sequence for rattlesnake is correct, there seems to be no easy way to explain it, short of conjuring up a vision of a lonesome cowboy on the lone prairie, with none but a rattlesnake for company [referring to the seeming similarity of its sequence to that of the genus *Homo*]." I think that there are better ways to explain that single discrepancy, even *if* the sequence is correct.

Cronquist presumably wants us to believe that an occasional unsteady tick (if even that!) in the animal world is sufficient reason to believe that this same clock is *largely* unsteady in the plant world. In his desire to discredit such data, at least that of cytochrome *c*, he likens this to the Age and Area concepts of Willis (ludicrous!), followed by the statement that:

> Evolution of other characters in both plants and animals tends to undergo periods of rapid radiation, interspersed with periods of more gradual change, and there is no *a priori* reason to suppose that adaptively significant changes in amino acid sequence would proceed any differently.

Of course, that's the point; there has been a sufficiently long record of plant evolution so as to believe that the cytochrome *c* clock has some kind of accuracy; fast or slow upon occasion, it nonetheless seems to average out as stochastic over time. Anyway, a generally erratic clock is better than no clock, giving the muddle of morphological darkness within which most plant taxonomists work.

As a final denouement, in case he hasn't convinced the reader, Cronquist adds a neat punch paragraph:

> This discussion of the evolutionary clock may be something like beating a dead horse, but some people are still trying to ride the horse. If the horse is really dead it won't mind the beating.

One should perhaps remind Cronquist that, to judge from the recent articles by Fitch (1976), Zuckerkandl (1976), King (this symposium), and articles in press by yet other such workers, the horse is alive, is being ridden quite nicely, and perhaps doesn't deserve the beating being administered!

It would be unfair to conclude this address with the audience feeling that Cronquist might be quite negative towards the application of chemical data to taxonomic problems. He is not, for he concludes, in hindsight, that:

> I welcome the appearance of amino acid sequences as an additional tool for taxonomists . . . . When we have the sequences for several proteins from members of a wide range of families, including critically important ones, we can make good use of this powerful tool.

Let's hope he means this; in the meantime he might wish to paraphrase Shakespeare's King Richard the Third, "A dead horse, a dead horse, *My Kingdom* for a dead horse!"

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SYSTEMATICS OF *MORAEA* (IRIDACEAE) IN TROPICAL AFRICA[1]

PETER GOLDBLATT[2]

ABSTRACT

Moraea, with 24 species, is well represented in tropical Africa, although the center for the genus is to the south in the winter rainfall region of southern Africa. Nine species are described for the first time. (*M. callista* Goldbl., *M. afro-orientale* Goldbl., *M. iringensis* Goldbl., *M. inyangani* Goldbl., *M. angolensis* Goldbl., *M. tanzanica* Goldbl., *M. upembana* Goldbl., *M. brevifolia* Goldbl., *M. balundana* Goldbl.) Only two of the five subgenera of *Moraea* occur in tropical Africa, subgenus *Vieusseuxia* and subgenus *Grandiflora*, the latter in particular exhibiting considerable radiation in south central Africa. On the basis of limited knowledge of morphological and cytological variation patterns in tropical Africa, *Moraea* is believed to be of recent origin here. Details of ecology, cytology, and evolution are elaborated and compared to patterns in southern Africa.

Moraea is a large genus of some 95 species, occurring throughout sub-Saharan Africa. The genus comprises small to medium-sized herbaceous geophytes. It is found mainly in highland areas in the tropics, usually in well-watered grassland, but also in open woodland or in marshy places. In temperate southern Africa, *Moraea* occurs at all elevations. *Moraea* is of some economic importance as all species are to some degree toxic to stock, section *Polyanthes* particularly so. Only a few species have been proven toxic, but all should be assumed to be until shown otherwise. The present revision treats only the tropical African members of the genus and will complete my taxonomic study of *Moraea*, begun in 1973 with a revision of *Moraea* in the summer rainfall region of southern Africa, followed by a revision of *Moraea* in the winter rainfall region of southern Africa (Goldblatt, 1973, 1976b).

This treatment includes as tropical Africa the area south of the Sahara and north of the region covered by the *Flora of Southern Africa* [Namibia (South West Africa), Botswana, Lesotho, Swaziland, and South Africa]. In this area, extending from Rhodesia north to Nigeria and Ethiopia, there are 24 species of *Moraea*, a larger number than previously recognized, but low in comparison to the 76 species in southern Africa. Only five species occur in both tropical and the southern African summer rainfall region, while one species, *M. spathulata*, occurs in the winter rainfall region of southern Africa as well. The present work is the first modern comprehensive treatment of *Moraea* in tropical Africa and the only treatment since Baker's (1898) revision for the *Flora of Tropical Africa*.

RELATIONSHIPS

The affinities and relationships of *Moraea* are discussed in detail in my revision of the species found in the winter rainfall region of southern Africa (Gold-

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blatt, 1976b) and also in a paper dealing with the cytology and subgeneric classification (Goldblatt, 1976a). In the latter paper I expanded my earlier hypothesis that *Moraea* is a relative of the widespread northern hemisphere *Iris* and that these two genera probably had a common origin from ancestors of the genus *Dietes*. *Moraea* is, however, more closely related to a group of South African corm-bearing genera which, like *Moraea*, also have a secondary bifacial leaf than to *Iris* or *Dietes*. These genera include *Homeria*, *Hexaglottis*, *Gynandriris*, *Galaxia*, and *Barnardiella* which are placed with *Moraea* in Homerinae (Goldblatt, 1976a), one of the three subtribes of Irideae, a predominantly Old World tribe of subfamily Iridoideae.

GEOGRAPHY OF THE TROPICAL AFRICAN SPECIES

Although *Moraea* occurs throughout sub-Saharan Africa, its present center is clearly the winter rainfall region of southern Africa which extends along the south and west coast of the Cape Province. Not only is this area richest with 54 species, 48 being endemic, but it is also the center of diversity in the genus. All five subgenera occur here and three of these are essentially endemic. The two largest subgenera *Vieusseuxia* and *Grandiflora*, also considered the more advanced, extend well outside the winter rainfall region. In fact, the center for subgenus *Grandiflora* lies outside this area, in the mountains of southeast Africa, extending from Natal to Malawi, Tanzania, and Zaïre.

Subgenus *Vieusseuxia*, the second subgenus found in tropical Africa, comprises two sections. Section *Polyanthes*, the less specialized, occurs from the southern Cape to Ethiopia and is well represented in Tanzania, as well as in the South African provinces of Natal and the Cape. The most primitive members of section *Polyanthes* are believed to be those with several leaves and unlimited branching, rather than single-leafed, few- or unbranched species; these include *M. polyanthos* and *M. polystachya* from the Cape Province and *M. carsonii* from Rhodesia-Zambia-Malawi. The center for this section thus may also lie in the mountains of southeast Africa but perhaps more likely to the south along the interface between the summer and winter rainfall regions. The second section of subgenus *Vieusseuxia*, section *Vieusseuxia*, is clearly specialized (Goldblatt, 1976b) and does not occur outside southern Africa where it is concentrated in the winter rainfall region.

In tropical Africa, *Moraea* occurs in almost all highland areas above 1,200 m and concentrations of species are found mainly in isolated areas that are considerably higher. Representation of the genus is notably poorer north of the equator with only two species in Ethiopia, three in the Uganda-Sudan-Kenya highlands, and only one in the mountains of eastern Nigeria and Cameroons. Significant areas of concentration are all in the highlands of central tropical Africa and several endemics occur in these isolated, and well-watered montane and semimontane regions. The main centers of endemism are as follows:

1. Inyanga highlands of Rhodesia: 5 species, one endemic (*M. inyangani*).
2. Northern Malawi-eastern Zambia escarpment and Southern Highlands of Tanzania: 8 species, 3 endemic (*M. tanzanica*, *M. callista*, *M. iringensis*).

3. North-central Zambia, southern and eastern Shaba: 14 species, 5 endemic (*M. brevifolia*, *M. unifoliata*, *M. balundana*, *M. bovonei*, *M. upembana*).

Subgenus *Vieusseuxia* is predominantly eastern in distribution and though it occurs from Ethiopia to Rhodesia, it does not extend anywhere in tropical Africa west of longitude 24°E, and is thus absent from Angola and the Nigeria-Cameroon highlands. Almost as wide ranging as subgenus *Grandiflora* in tropical Africa, subgenus *Vieusseuxia* is poor in species, with only 7 species north of South Africa, and only 4 of these exclusive to tropical Africa. Significant speciation in subgenus *Vieusseuxia* occurs only in the Southern Highlands of Tanzania where two very striking species, *M. callista* and *M. iringensis*, are endemic. Other species of subgenus *Vieusseuxia* are widespread, with *M. thomsonii* extending over almost the entire range of the subgenus in tropical Africa, and found from Ethiopia in the north to Transkei in southern Africa.

Subgenus *Grandiflora* is well represented in tropical Africa by 16 species, only two also found in South Africa where an additional 11 species occur. The only really widespread species of this subgenus in tropical Africa is *M. schimperi* which extends over the whole range of *Moraea* in tropical Africa. Other species are considerably more restricted, and several species are known from single collections or a very small area. *Moraea inyangani* is one example while several species in the *M. tanzanica-M. unifoliata* alliance of reduced species are also very local, especially *M. unifoliata*, *M. balundara*, *M. bovonei*, all from Shaba, Zaïre, *M. brevifolia* in northeastern Zambia, and *M. tanzanica* in southwestern Tanzania-northern Malawi. A very marked center of speciation for subgenus *Grandiflora* is evident in this belt across south-central tropical Africa.

History

The first collections of *Moraea* from tropical Africa were made as early as the 1840s when Schimper discovered *M. schimperi* in Ethiopia. Schimper's collections were first assigned to two separate species in the genus *Hymenostigma*. Knowledge was later extended by Welwitsch who collected *M. schimperi*, *M. clavata*, and *M. textilis* in Angola in the years following 1853. Welwitsch's Angolan Iridaceae were only described much later, in 1878, by Baker who actually admitted seven species from Angola including three now regarded as conspecific, and referred to *Ferraria* rather than *Moraea*.

The important milestone in the knowledge of *Moraea* in tropical Africa is J. G. Baker's (1898) treatment for *Flora of Tropical Africa*. Baker recognized 16 species in his treatment. However, four of these are clearly the same species of *Ferraria*, *F. glutinosa*, one is today regarded as *Dietes*, while of the remaining 11 species *M. welwitschii*, *M. zambeziaca*, and *M. diversifolia* are conspecific (*M. schimperi*) and another two, *M. textilis* and *M. mechowii*, are also regarded here as the same species. A last species, *M. bella*, was until recently associated with the Cape endemic *M. angusta*, although it is in fact unrelated. By 1898 only seven of the presently recognized species were known, six were named and one misidentified.

Subsequent studies on *Moraea* were carried out independently by German,

Belgian, and British botanists who confined their interests largely to the colonies of their respective countries. In particular, de Wildeman, working on the flora of what is now Zaïre and Burundi, described six species, all new for the Congo, but four of which have proved to be synonyms of earlier species from other parts of tropical Africa. More recently, *Moraea* has received very little systematic attention in tropical Africa. In fact, the recent treatment by Geerinck (1970) for Zaïre and Burundi is the only significant work in the last fifty years. Geerinck recognized six species, one tentatively; and subsequently one more (Geerinck, 1972). Geerinck's species concepts were far broader than those held by me and I recognize several more species in the Zaïre-Burundi area than Geerinck did. In the present revision 9 of the 24 species are new to science. Knowledge of the genus in tropical Africa is, however, far from satisfactory, and several species are known from one locality while collections of some species are incomplete, lacking corms or fruits or adequately preserved flowers.

ECOLOGY

HABITAT

Moraea occurs in two distinct types of habitat in tropical Africa, either in dry situations in grassland and open woodland or in wet, marsh situations known in southern Africa as vleis, and in south tropical Africa as dambos. Dambos may be seasonal or permanent, but have the characteristic of being poorly drained yet seldom deep, and usually have a rich vegetation including many grasses, sedges, as well as geophytes and herbaceous dicots. The dry habitat may comprise more than a single niche for *Moraea*, but data available does not indicate this, rather suggesting that species may be fairly tolerant of minor ecological differences and thus growing equally well in open woodland or grassland of various types. Most species, though not all, appear to be restricted to either one or other of the two major habitats. Records suggest that *M. ventricosa* and *M. textilis* are exceptions, as they are listed as having been collected in woodland, grassland, or on the edges of marshes. Personal observation has shown that *M. schimperi* also occurs from wet marshes to open, well-drained grassland, the latter habitat being occupied only in areas of higher rainfall.

FLOWERING TIME

Species of *Moraea* may be found in bloom almost throughout the year, though few species flower in the dry season. Peak blooming time is mid wet season. Each species, however, has its own fairly limited flowering period, and detailed examination of flowering times suggests that this factor is of considerable significance in the evolution of the genus in tropical Africa. In general, it appears that only a few species, and only one in each subgenus, may bloom in a particular habitat in any given locality at one time. Species of *Moraea* tend to bloom for about two months; thus in a particular area several species might occur, each flowering at a different time. The significance of flowering times is elaborated further in the following discussion on evolution.

Evolution

The pattern of species that prevails in *Moraea* in tropical Africa suggests that the group is rapidly evolving into a limited number of spatial, temporal, and ecological niches available to the genus. A very limited degree of important floral differences suggests that there has not been sufficient time for fundamental morphological changes to become established in the flowers, so that selection for different pollinators has not been accomplished.

There are three major groups which are dealt with separately in the following discussion: the large-flowered *M. spathulata-M. textilis* series of subgenus *Grandiflora*; the smaller flowered and morphologically specialized *M. tanzanica-M. unifoliata* series of subgenus *Grandiflora*; and the small uniformly blue-flowered subgenus *Vieusseuxia.*

1. The *Moraea spathulata-M. textilis* series.

The series comprises vegetatively similar, large-flowered species in which both flowering time and habitat differences have played the major role in their evolution.

The dry habitat does not support species of subgenus *Grandiflora* in the dry season, with the possible exception of the poorly known September-blooming *M. upembana.* Early in the wet season, from December, *M. verdickii* blooms in Tanzania, Zambia, and Zaïre. *Moraea ventricosa* follows in this region with a blooming peak in March. Subsequently, at least in the east, in Malawi and Tanzania, *M. macrantha* blooms from March to June, lasting into the beginning of the dry season.

In the wet habitat, the wide-ranging *M. schimperi* blooms from September to early December south of the equator. It is replaced later in the season by a variety of more localized species of the series dealt with in the following section, including *M. brevifolia* in Zambia, *M. unifoliata*, *M. bovonei*, and *M. balundana* in Zaïre. Later, towards the end of the wet season, *M. bella* blooms in Zambia, Zaïre, Malawi, and Tanzania.

Geographical isolation is of relatively minor significance in the evolution of this series but has played a role as in *M. ventricosa-M. textilis*, which occupy similar habitat and temporal niches but have different geographical ranges. A similar role for geographical isolation is seen for *M. verdickii-M. spathulata.*

2. The *Moraea tanzanica-M. unifoliata* series.

The species of this series are all relatively small in size, have similar yellow flowers, and exhibit distinctive vegetative modifications making them easy to recognize. Unlike the previous series, all, with the exception of the poorly understood *M. upembana*, occupy a similar habitat and flower at the same time. Spatial isolation is the major factor of evolutionary significance here, with each species relatively limited in range and none sympatric. Small, local populations are characteristic in the series.

3. Subgenus *Vieusseuxia.*

Subgenus *Vieusseuxia*, also a group where species have very similar flowers, exhibits a similar pattern of evolution to subgenus *Grandiflora* with ecological factors assuming dominance over a secondary geographic element. The dry

grassland habitat supports *M. thomsonii* in the later dry season; *M. carsonii* in the early to mid wet season at least in the south; *M. afro-orientale* in similar situations north in Tanzania, Kenya and Uganda; and *M. iringensis* locally. In the wet habitat, *M. natalensis* blooms in the wet season throughout south tropical Africa. There are no late-blooming species and presumably taller grasses shade out these smaller plants in late season.

The exception to the patterns described above is the very striking *M. callista*. This species has a large and very different flower from its allies and, although it presumably evolved in isolation, it is now distinguished by its floral peculiarities and, by inference, has a distinctive series of pollinators.

Summarizing, two main modes of evolution appear to have been operative in the tropical African species of *Moraea*. These are: (1) an ecological factor (habitat and flowering time) and (2) a geographical (spatial) factor. Within the two major groups, subgenera *Grandiflora* and *Vieusseuxia* (excluding *M. callista*), floral differences are small and probably not of adaptive significance, so that the species of each group do not appear to have evolved in response to pressures from pollinators.

This situation is similar in the summer rainfall area of southern Africa, although somewhat more complex, with more species and basic types, and an element of floral evolution is evident in section *Vieusseuxia*. However, the evolutionary pattern in the winter rainfall region is quite different. Flowers vary considerably and floral adaptation is of the greatest significance. Evolution for limited and specific ranges of pollinators consequently must have been important. Flowering time and habitat are minor as most species grow in essentially similar situations and all are spring blooming. Soil differences assume great importance as does the geographical factor. Related species are often isolated from one another geographically or by distinct soil preferences. The evolutionary patterns here, in fact, are typical of an area with a Mediterranean climate (Raven, 1973).

Taxonomic Characters

The morphology and important taxonomic characters were dealt with at length in my recent paper on *Moraea* in the winter rainfall region of southern Africa and little need be added here. It will, however, be helpful if I summarize the important features of the two subgenera that occur in tropical Africa.

Subgenus *Grandiflora* comprises the largest-flowered species in the genus, though a few specialized species in tropical Africa—e.g. *M. clavata*, *M. angolensis*, and *M. unifoliata* have relatively small flowers. Floral morphology is uniform apart from size and color, most species having yellow flowers, only *M. schimperi*, *M. ventricosa*, *M. macrantha* and *M. textilis* having blue flowers. Outer tepals are outspread, the inner ± erect. All species are unbranched, and have a single leaf, usually well developed and basal, but in a few species reduced and inserted well above ground level. All species in which fruits are known have large flattened ± discoid seeds and large capsules. The subgenus extends from the southern Cape in South Africa to Nigeria and Ethiopia but

TABLE 1. Chromosome number in tropical African *Moraea*. An asterisk (*) indicates a count for South African material only; new counts are in bold type.

Species	Diploid number 2*n*	Collection data or reference
M. carsonii	12	Goldblatt, 1976a
M. elliotii	12*, 24*	Lewis, 1966; Goldblatt, 1976a.
M. natalensis (as *M. erici-rosenii*)	12	Lewis, 1966.
M. thomsonii (as *M. stricta*)	12	Chimphamba, 1974.
	48	Malawi, Zomba Mt., *Goldblatt s.n.* (no voucher).
	24*, 36*	Goldblatt, 1971.
M. spathulata (incl. subspp.)	12*	Goldblatt, 1971, 1976a.
M. schimperi	12	Goldblatt, 1971; Chimphamba, 1974. Malawi, Zomba Mt., *Goldblatt 4259* (MO). Malawi, Chikangawa-Mzuzu, *Goldblatt 4590* (MO). Malawi, Mzuzu, Marymount, *Pawek 5833* (MO).
M. *macrantha* (as *M. textilis*)	12	Goldblatt, 1976a.
	12	Malawi, Mzuzu, *Pawek 5396* (MO). Malawi, Katumbi-Nyika intersection, *Goldblatt s.n.* (no voucher).
M. ? ventricosa (flowers not seen)	**12**	Burundi, Mt. Bona, E. Bujumbura, *Goldblatt s.n.* (no voucher).
M. tanzanica	**12**	Malawi, Nyika Plateau, Juniper forest road, *Pawek 6660* (MO).

is notably absent from the southwestern Cape, an important center for the genus as a whole.

Subgenus *Vieusseuxia*, composed of two sections of which only section *Polyanthes* occurs outside South Africa, comprises small to fairly large plants all with very similar blue (to white) flowers, which in tropical Africa are quite small and in marked contrast to subgenus *Grandiflora*. Tepals of both whorls are outspread, the exception being *M. callista* from southwestern Tanzania which has unusual, large blue and white flowers with reflexed tepals. Species vary in leaf number and position of insertion which ranges from basal to just below the inflorescence in *M. natalensis*. *Moraea carsonii* has 2–3 leaves, *M. callistra* has two, while other species typically have one leaf. Seeds of all species, where known, are small and angular and capsules are small. The subgenus extends from the southwestern Cape to Ethiopia but is absent from West Africa and Angola. Section *Polyanthes* is the more widespread, with section *Vieusseuxia* restricted to Africa south of the Limpopo.

CYTOLOGY

Moraea is well known chromosomally (Goldblatt, 1976a), some 65% of the 95 species having been studied. It is least well known in tropical Africa and only 9 of the 24 species have now been counted. Counts for the genus in tropical Africa are summarized in Table 1, where several new counts are presented.

The tropical African species have fairly uniform karyotypes, with a base number of $x = 6$. The chromosome complement in all species of subgenus *Grandiflora* examined is similar and all species are diploid, $2n = 12$, with 4 large telocentric pairs, and two ± acrocentric pairs. Satellites are located on a telocentric pair (Goldblatt, 1976a: 13). *Moraea schimperi* is distinctive in having a secondary constriction on the end of the long arm of an acrocentric pair, a feature also noted by Chimphamba (1974).

In subgenus *Vieusseuxia* the chromosomes are acrocentric with the longest pair almost metacentric (Goldblatt, 1976a: 13). Polyploidy has been reported in both sections. In section *Polyanthes*, *M. thomsonii* is heteroploid with tetraploid and hexaploid plants recorded in South Africa and an octoploid from Malawi. Chimphamba (1974) has reported $2n = 12$ in this species but determination needs to be confirmed and the locality is unknown. *Moraea elliotii* is also heteroploid, with diploidy and tetraploidy reported in South African plants.

The cytological uniformity of *Moraea* in tropical Africa, especially in subgenus *Grandiflora*, contrasts with a great degree of heterogeneity in South African winter rainfall area species. This uniformity supports my suggestion based on limited morphological variation that *Moraea* is of fairly recent origin in tropical Africa.

TAXONOMIC TREATMENT[3]

Moraea Miller, Figs. Pl. 159, *tab. 238.* 1758, as *Morea* and altered to *Moraea* by Linnaeus, nom. cons. TYPE: *M. vegeta* L.

For complete synonymy and generic description see Goldblatt (1976b).

Distribution: Sub-Saharan Africa, in highland areas in the tropics, at all altitudes in temperate southern Africa; species concentrated in South Africa, mainly in the southwestern winter rainfall region.

KEY TO THE SPECIES

1. Produced leaves 2 or more, well developed.
    2. Sheathing portion of upper (cauline) leaf more than 1.5 cm long.
        3. Stem few to many branched; spathes 2.5–5 cm long .... 1. *M. carsonii*
        3.′ Stem simple or 1-branched; spathes 4–6 cm long .... 2. *M. callista*
    2.′ Sheathing portion of upper leaf 2–6 mm long .... 3. *M. afro-orientale*

1.′ Produced leaf solitary, occasionally reduced and ±bractlike or lacking at flowering time.
    4. Plants either leafless at flowering time, or with a dry withered leaf attached; blooming in the dry season.
        5. Flowers yellow; outer tepals 2.7–4.5 cm long .... 21. *M. upembana*
        5.′ Flowers pale blue violet; outer tepals 1.5–2.2 cm long .... 7. *M. thomsonii*

[3] All major collections of African flora were consulted for this study, and unless otherwise stated all type specimens were seen. Field work was carried out in Malawi and to a limited degree in Rhodesia.

Specimens examined are generally arranged in accordance with modern floristic projects for particular areas. Modern place names are used, but old names where well known or recently altered, are provided in parentheses.

Collection data or literature citation for chromosome numbers in the descriptions are given in the section on CYTOLOGY.

4.′ Plants with a green produced leaf at flowering time, usually well developed but occasionally very short and inserted just below the inflorescence.
6. Leaf inserted immediately under the inflorescence (leaf sometimes bract-like and almost entirely sheathing).
7. Flower blue; stem usually branched .... 6. *M. natalensis*
7.′ Flowers yellow; stem simple.
8. Outer inflorescence spathe only slightly shorter than the inner.
9. Leaf barely distinguishable from the spathes and not or only shortly exceeding them .... 24. *M. unifoliata*
9.′ Leaf several times longer than the spathes .... 22. *M. bovonei*
8.′ Outer inflorescence spathe less than half as long as the inner .... 23. *M. balundana*
6.′ Leaf inserted from the base to the upper part of the stem but not immediately below the inflorescence.
10. Outer tepals 1.4–3.5 cm long.
11. Sheathing portion of bract leaves at least 1.5 cm long.
12. Flowers blue; outer tepals 1.4–2.5(–3.0) cm long.
13. Leaf inserted in the upper third of the stem 6. *M. natalensis*
13.′ Leaf inserted in the lower third of the stem 5. *M. elliotii*
12.′ Flowers yellow; outer tepals (2.0–)2.5–3.5 cm long.
14. Bract leaf solitary .... 20. *M. clavata*
14.′ Bract leaves 3 or 4.
15. Spathes 5–8 cm long; bract leaves 5–8 cm long .... 11. *M. inyangani*
15.′ Spathes 4.5–5.5 cm long; bract leaves 3.0–4.5 cm long .... 12. *M. angolensis*
11.′ Sheathing portion of bract leaves 1–7 mm long.
16. Ovary 3–5 mm long; anthers 4–5 mm long .... 3. *M. afro-orientale*
16.′ Ovary 7–13 mm long; anthers ±6 mm long .... 4. *M. iringensis*
10.′ Outer tepals 3.8–10 cm long.
17. Bract and spathes ±dry at flowering time and the flowers blue and blooming at the end of the dry season to early in the wet season (Sep.–Dec. south of the equator, Dec.–May north of the equator); leaf often shorter than the stem, the prophylls dark brown and prominent .... 9. *M. schimperi*
17.′ Bracts and spathes at least partly herbaceous at flowering time, or if not, the flowers white to yellow and not flowering at the end of the dry season; leaf exceeding the stem, or if not, flowers white to yellow.
18. Leaf inserted above ground level, very short and rarely exceeding the spathes, the bract leaves usually solitary .... 19. *M. brevifolia*
18.′ Leaf ±basal or if inserted well above the ground, then the bract leaves 1 or 2, the leaves not exceeding the spathes or the plants no more than 35 cm high.
19. Plants of Rhodesia, southern Mozambique (and South Africa).
20. Flowering in spring and early summer, Sep.–Nov., usually in moist habitats; 30–50(–70) cm tall; leaf ca. 5 mm wide .... 10. *M. muddii*
20.′ Flowering in summer in open grassland; usually more than 50 cm tall; leaf usually more than 1 cm wide .... 8. *M. spathulata*
19.′ Plants of Angola and occurring north of Rhodesia and southern Mozambique.
21. Plants 30–35 cm tall with 2 bract leaves only and the leaf only shortly or not exceeding the spathe .... 18. *M. tanzanica*
21.′ Plants usually more than 40 cm tall, if less, then the bract leaves more than 2 and the leaf much exceeding the spathes.

22. Bracts not overlapping.
    23. Flowers blue.
        24. Outer tepals 5.5–8 cm long; corm tunics of pale, reticulate fibers; plants of Zaïre, Tanzania, Zambia, Malawi .... 15. *M. macrantha*
        24.' Outer tepals 4.7–6 cm long; corm tunics of wiry, dark fibers; plants of Angola .... 17. *M. textilis*
    23.' Flowers yellow.
        25. Flowering Nov. to Feb. (Mar.), usually in open grassland; anthers 10–14 mm long; outer tepals 5–10 cm .... 14. *M. verdickii*
        25.' Flowering (Feb.) Mar. to July in damp situations; anthers 8–10 mm long; outer tepals 4.5–5.5(–6.5) cm .... 13. *M. bella*
22.' Bracts overlapping.
    26. Flowers blue.
        27. Outer tepals more than 5.5 cm long .... 15. *M. macrantha*
        27.' Outer tepals less than 5.5 cm long.
            28. Anthers 8–10(–11) mm long; inner tepals 3.7–4.5 cm long; plants of Zaïre, Zambia, Burundi, Tanzania .... 16. *M. ventricosa*
            28.' Anthers (10–)10.5–15 mm long; inner tepals 4.8–6.5 cm long; plants of Angola .... 17. *M. textilis*
    26.' Flowers white to yellow.
        29. Anthers 8–10 mm long; bract number 3–4(–5) .... 16. *M. ventricosa*
        29.' Anthers 10–15 mm long.
            30. Outer tepals 5–10 cm long; bract leaves 2–3(or 4 but then the tepals more than 5 cm) .... 14. *M. verdickii*
            30.' Outer tepals 4.5–6.5 cm long; bract leaves (4–)5–7 .... 17. *M. textilis*

Subgenus VIEUSSEUXIA (de la Roche) Baker—Section POLYANTHES Goldbl.

1. **Moraea carsonii** Baker, Bull. Misc. Inform. 1894: 391. 1894. TYPE: Zambia, Mbala (Abercorn) district, "Fwambo," *Carson s.n.* (K, holotype).—FIG. 1A.

M. homblei De Wild., Contr. Fl. Katanga, Suppl. 4: 7. 1932. TYPE: Zaïre, Shaba (Katanga), near Kolwezi, *Homblé 1024* (BR, holotype).

Plants small to medium in size, 20–40 cm high, usually bearing several branches. *Corm* ca. 1.5 cm in diameter; tunics of dark brown, fine to medium reticulate fibers. *Prophylls* dry and papery, pale brown, the upper often torn somewhat distally, occasionally becoming fibrous. *Leaves* 2, occasionally 3, the lower ±basal or inserted well below the branches, the upper cauline, canaliculate, 2–5 mm wide, usually falcate, exceeding the infloresence; sheath of upper leaf 1.5–2 cm long. *Spathes* occasionally reddish, herbaceous below, becoming dry from the apex, the margins dry, pale brown, the apices dark brown, attenuate; inner spathe 3.2–5.0 cm long, the outer about two-thirds the inner.

FIGURE 1. *Moraea* species.—A. *M. carsonii*.—B. *M. afro-orientale*. (×0.5).

Flower blue with yellow nectar guides; *outer tepals* 2.1–3 cm long, lanceolate spreading, the limb slightly longer than the claw; *inner tepals* 2–2.8 cm long, spreading. *Filaments* ca. 7.5 mm long, free in the upper third; *anthers* 4.5–5.5 mm long. *Ovary* 3.5–7 mm long; style branches 8 mm long, the crests 7–10 mm long. *Capsule* ovoid, to 8 mm long; *seeds* small, angular. Chromosome number $2n = 12$.

Flowering time: December to February.

Distribution: Rhodesia, Zambia, Malawi, southern Zaïre.—FIG. 2.

Its two or sometimes three leaves, indeterminate growth pattern with several to many branches and small unspecialized flowers, place *M. carsonii* in a primitive position among the tropical African species of the genus. It clearly belongs in subgenus *Vieusseuxia* section *Polyanthes* and is probably most closely allied to the South African, southern Cape species, *M. polyanthos*, which generally has three leaves and similar flowers, and also to the widespread southern African *M. polystachya*, a taller species with much larger flowers. *Moraea carsonii* appears to represent a link between these two multi-leafed southern African species and the several tropical and South African summer rainfall region species of section *Polyanthes*, most of which have a very similar flower but only a single leaf, and are distinguished mainly by differences in growth form.

Moraea carsonii has a relatively wide range, occurring in the Zaïre province of Shaba (Katanga), in northern and eastern Zambia, and adjacent Malawi. A somewhat different form is found to the south in the Inyanga highlands of Rhodesia, which is generally more robust, and has larger flowers, giving it a resemblance to *M. polystachya* to which it is frequently referred. Not all plants from Inyanga are equally robust, and several collections cannot be distinguished from plants occurring further north. For this reason the Inyanga populations are not accorded taxonomic recognition here.

In Tanzania and northwards to the Sudan *M. carsonii* is replaced in similar habitats by *M. afro-orientale* Goldbl., which has until now been included in *M. carsonii* (Burtt, 1938). *Moraea afro-orientale* differs in having a single basal leaf inserted below ground, smaller flowers, and fewer branches which are often clustered in umbellate fashion. Occasionally, particularly in southern Tanzania, forms occur with two leaves but the upper leaf has an unusually short sheath.

MALAWI. NORTHERN REGION: Mtwalo-Mzimba road, *Pawek 3358* (K, MAL). Vipya hills S of Mzuzu, *Pawek 4421* (K). SW Mzuzu, *Pawek 8051* (MO, SRGH). 5 km S Mt. Hora, Rumphi district, *Hillard & Burtt 4456* (K, MAL, SRGH). CENTRAL REGION: Kongwe Mt. near Dowa, *Robson 1654* (BM, LISC, PRE, SRGH).

RHODESIA. EASTERN REGION: Mt. Inyangani, *Plowes 2153* (PRE, SRGH); *Davidse, Simon & Pope 6536* (MO); *Norlindh & Weimarck 4968* (BM, BR, K, PRE, SAM); *West 7010* (SRGH); *Wild 4927* (K, LISC, MO, PRE, SRGH). Near Bonda Mission, *Wild 5478* (COI, K, MO, PRE, SRGH). Above Rhodes Hotel, Inyanga, *Whellan & Davies 997* (SRGH). Nyamaropa Forest Reserve, Inyanga, *Dale SKF204* (K, SRGH); *Drewe 28, 54* (SRGH); *Wild 7495* (BR, K, LISC, PRE, SRGH, MO). Inyanga Downs, *Wild 5475* (K, MO).

ZAÏRE. SHABA: 10 km S of Lubumbashi (Elizabethville), *Schmitz 1286* (BR). Lubumbashi, *Salèsiens 1062* (BR). Fungurume, *Symoens 14023* (BR, K).

ZAMBIA: CENTRAL REGION: Lusaka, *Angus 1466* (K, LISC, SRGH). Kafue River, *Allen 498* (K, SRGH). Kundalila Falls, Serenje district, *Strid 2900* (K). NORTHERN REGION: Mbala township, *Sanane 986* (K). Near Nakatali, *Richards 8023* (K). Kalambo Falls, Mbala

(Abercorn), *Richards 3933* (K). Sansia Falls, Mbala district, *Richards 7436* (K). Mbesuma ranch, *Astle 1185* (K, SRGH). WESTERN REGION: Luanshya, *Fanshawe 1739* (BR, K, SRGH). Mufulira, *Fanshawe 11749* (SRGH). Ndola, *Fanshawe 612* (BR, K).

2. **Moraea callista** Goldbl., sp. nov. TYPE: Tanzania, Southern Highlands, Elton Plateau, *Richards 7562* (K, holotype; BR, isotype).—FIG. 3A.

Planta 30–70 cm alta. *Cormus* ignotus. *Folia* duo, canaliculata, inferius basale, caulis simplex vel uniramosus. *Spathae* inflexae, herbaceae, exterior 4–6 cm longa, interior 3–4.5 cm longa. *Flores* caeruleo-malvini, tepala albescentes distale; *tepala exteriora* 3–3.5 cm longa, limbis 2–2.5 cm longis, reflexis; *interiora breviora*, reflexa. *Filamenta* ad 8 mm longa; *antherae* 6 mm longae. *Germen* 5–7 mm longum; rami styli ca. 8 mm longi; cristae 5–7 mm longae.

Plants solitary, simple or rarely 1-branched, 30–70 cm high. *Corm* not known. *Prophylls* membranous, the uppermost dry and fibrous towards the apex. *Leaves* 2, the lower basal and larger, the upper cauline, to 7 mm wide, canaliculate with slightly thickened hyaline margins, as long as, or slightly exceeding the inflorescence. *Spathes* often inflexed, herbaceous, with dry upper margins; outer spathe 4–6 cm long, the inner ca. ⅔ the inner. *Flowers* blue mauve with the tepals fading to white distally; *outer tepals* 3–3.5 cm long, the limb 2–2.5 cm, fully reflexed when open; *inner tepals* somewhat smaller, also reflexed. *Filaments* to 8 mm long, united in the lower 5 mm; *anthers* 6 mm long. *Ovary* 5–7 mm long; style branches ca. 8 mm long, very broad and outspread, the crests 5–7 mm. *Capsule* and *seeds* unknown. Chromosome number not known.

Flowering time: January to February in the west, May in the east.

Distribution: Southwestern and eastern Tanzania in mountain grassland, 1,800–3,000 m.—FIG. 2.

Moraea callista stands apart from the other species in section *Polyanthes* because its large striking flower with blue and white, fully reflexed tepals are quite distinct from the usual small, uniformly blue flowers with spreading tepals of other species. It occurs in two widely separated areas, high mountain grassland in the Njombe area in the southwestern part of Tanzania, and to the east in the Uluguru mountains where only one gathering has been made, flowering at a much later date, in May, compared to January and February in the western part of its range. The species is known from very few collections and is all too little understood.

TANZANIA. SOUTHERN HIGHLANDS: Elton Plateau, *Procter 1646* (EAH); *Richards 7562* (BR, K). Mangale-Njombe road, *Richards 14216* (K). Mwakete, Njombe district, *Richards 7823* (K). MOROGORO DISTRICT: Mzumbi, *Semsei 1707* (EAH, K, PRE).

3. **Moraea afro-orientale** Goldbl., sp. nov. TYPE: Uganda, Northern Province, Mt. Debasien, *Hedberg 1953* (UPS, holotype; EAH, K, S, isotypes).—FIG. 1B.

Planta 15–40 cm alta, gracilis. *Tunicae* cormi brunneae, reticulatae, tenuis. *Folium* solitarium, basale, raro folio secundo caulino, canaliculatum. *Caulis* ramosus, ferens bracteae sole vel folio caulinum unum, vagina brevissima. *Spathae* herbaceae, interior 2–3.5 cm longa, exterior 1–2 mm brevior. *Flores* caerulei; *tepala exteriora* 1.8–2.6 cm longa, effusa; *tepala interiora* 1.5–1.8 cm longa. *Filamenta* ca. 5 mm longa; *antherae* ca. 4.5 mm longae. *Germen* ad 8 mm longum; rami styli ca. 5 mm longi; cristae ad 5 mm longas.

Plants small, solitary, usually few branched, 15–40 cm high. *Corm* ca. 1.5 cm in diameter; tunics brown, cancellate to reticulate, of medium to fine fibers.

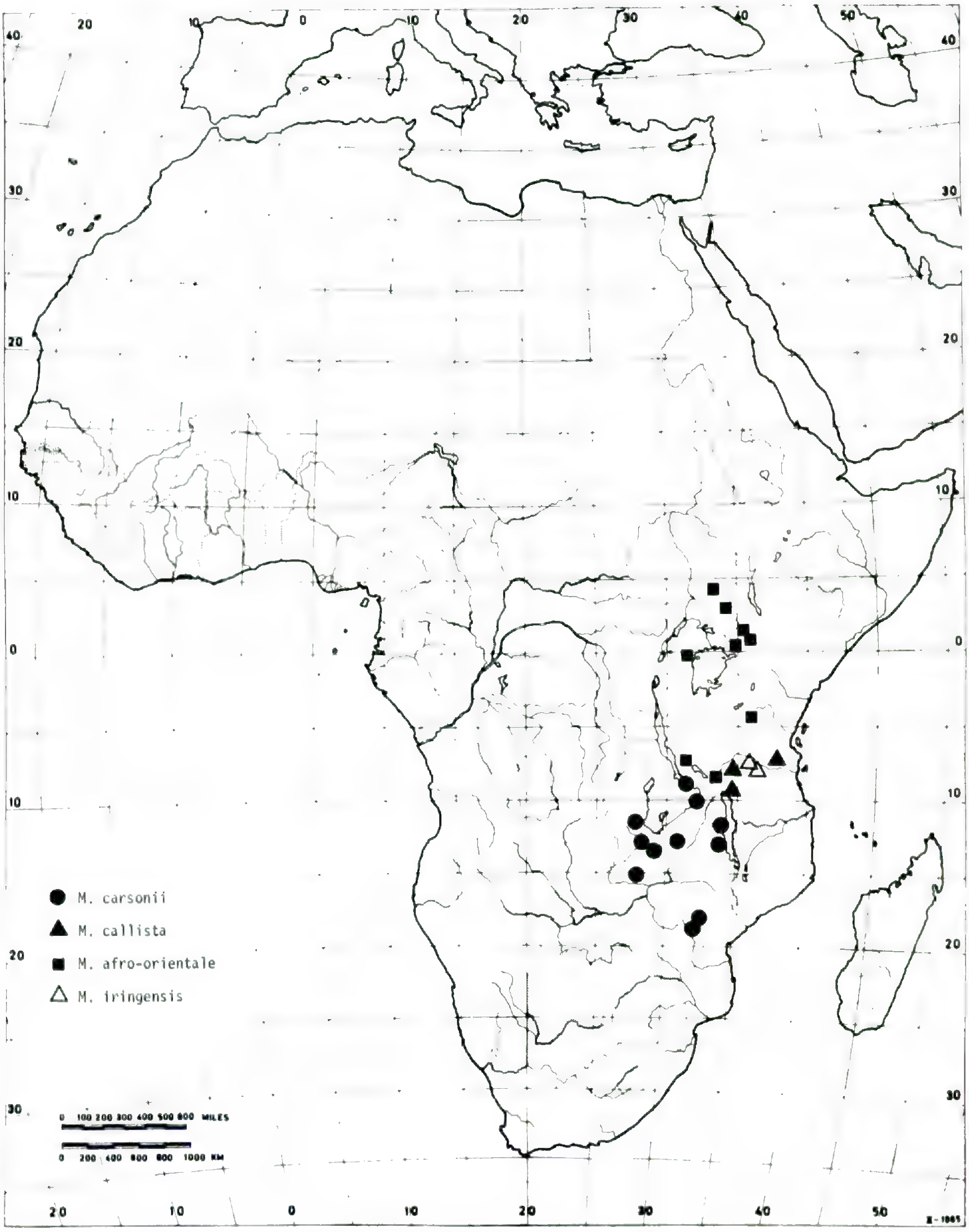

FIGURE 2. Distribution of *Moraea carsonii*, *M. callista*, *M. afro-orientale*, and *M. iringensis*.

Prophylls usually 3, membranous, entire, obtuse-truncate. *Leaf* usually solitary, basal, inserted below the ground, the base covered by prophylls, canaliculate, 2–5 mm wide, relatively short, as long as or slightly exceeding the inflorescence; occasionally a second leaf developed at the first aerial node, usually

bractlike, but 2–10 cm long, occasionally also exceeding the inflorescence; cauline leaf sheath 3–6 mm long. *Spathes* subequal, herbaceous, the margins membranous, rarely dry but not brown, the apices acute, brown tipped; inner spathe 2–3.5 cm long, the outer 1–2 mm shorter. *Flowers* blue with orange nectar guides; *outer tepals* 1.8–2.6 cm long, lanceolate, the limb slightly longer than the claw, spreading; *inner tepals* 1.5–1.8 cm long. *Filaments* ca. 5 mm long, free in the upper third; *anthers* ca. 4.5 mm long. *Ovary* 3–5 mm long; style branches ca. 5 mm long, the crests to 5 mm. *Capsule* ovoid, to 8 mm long; *seeds* small, angular. Chromosome number not known.

Flowering time: April to May north of the equator in Kenya, Uganda, and Sudan; December to January south of the equator.

Distribution: Southern Sudan, western Kenya, Uganda, and central and western Tanzania; in short grass and often in seasonally waterlogged ground, blooming soon after the start of the rainy season.—FIG. 2.

Moraea afro-orientale is closely allied to *M. carsonii*, from which it is probably derived, and it has until now been included in this species. It differs, however, in several respects and is distinctive in overall habit, with prominent membranous prophylls, short stem and few, often clustered branches. Most forms have only a single comparatively short and erect leaf, inserted below ground level in contrast with the two long, flaccid leaves in *M. carsonii*. In the southern part of its range, in central and western Tanzania, *M. afro-orientale* often has two leaves, but when this is the case, the upper, cauline leaf is always distinctive in having a very short sheath (2–5 mm), contrasting with the more usual longer sheath (10–20 mm) in *M. carsonii* and its other relatives. In the single-leafed northern forms of *M. afro-orientale* the second leaf is reduced to a bractlike structure, often with a short free apex, and this bract also has a very short sheath.

Moraea afro-orientale shares this distinctive, very short leaf or bract sheath with two other tropical African species, *M. iringensis*, which has a larger flower and a long ovary which is included in the spathes, and *M. callista*, which has two large leaves, and a large striking flower with blue and white, fully reflexed tepals. Both these species occur rather locally in southwestern and central Tanzania on the southern extremity of the range of *M. afro-orientale* (Fig. 2).

KENYA. NYANZA PROVINCE: Bungoma district, *Kokwaro 134* (EAH). SE slopes of Mt. Elgon, *Padwa 16* (EAH, F, K, PRE, SRGH). RIFT VALLEY PROVINCE: Elgon and Trans Nzoia, *Tweedie 444* (K). Kitale-Suam Mill road, *Bally 2487* (K). Slopes above Endebess, *Polhill 411* (BR, K, PRE). Mt. Elgon, *Rayner 545* (K); *Lugard 573* (K); *Adamson 513* (EAH, K). Endebess, *Webster 9018* (EAH).

SUDAN. EQUATORIA: Mt. Lotuke, Didinga Mts., *Jackson 1333* (BM); *MacDonald 91* (BM); *Myers 10952* (K).

TANZANIA. CENTRAL PROVINCE: Singida-Dodoma, *Feirarzl 5708* (EAH). SOUTHERN HIGHLANDS: Igurussi, Mbeya district, *Procter 2284* (EAH, K). Ruaha National Park, Magangwe Hill, *Bjornstad 2231* (EAH, K). WESTERN PROVINCE: Moanzi, Sumbawanga district, *Vezey-FitzGerald 1378* (K, SRGH). Kuturia-Lukunga confluence, Ufipa district, *Richards 10259* (BR, K). Above Malonje, near Sumbawanga, *Richards 7210* (K).

UGANDA. BUGANDA PROVINCE: Mengo, *Dradu 846* (EAH). EASTERN PROVINCE: Butiro, *Liebenberg 846* (K). NORTHERN PROVINCE: Karamoja district, Lodoketeminit, near Moroto, *Kerfoot 995,4947* (EAH, K). Mt. Debasien (Kadam), *Hedberg 1953* (EAH, K, S, UPS). Moruita, *Eggeling 5785* (BR, K). Karamoja, *Thomas 2836* (BR, K).

FIGURE 3. *Moraea* species.—A. *M. callista.*—B. *M. iringensis.*—C. *M. natalensis.* (×0.5)

4. **Moraea iringensis** Goldbl., sp. nov. TYPE: Tanzania, Southern Highlands, Kyimbila-Tandala, *Stolz 2362* (K, holotype; BM, BR, PRE, isotypes.)—FIG. 3B.

Planta 15–30 cm alta. *Folium* solitarium, basale, usitate parum inflorescentium brevior, canaliculatum. *Caulis* pauciramosa ferens bractea una vaginis brevissimus. *Spathae* herbaceae, interior 3–4.5 cm longa, exterior 1.5–2.3 cm longa. *Flores* caerulei; *tepala exteriora* ca. 3 cm longa, effusa; *interiora* ca. 2 cm longa, effusa. *Filamenta* ca. 7 mm longa; *antherae* ad 6 mm

longas. *Germen* 8–12 mm longum, non exsertum; rami styli ca. 1 cm longi; cristae ad 8 mm longas.

Plants solitary, (10–)15–30 cm high, usually branched. *Corm* ca. 1 cm in diameter; tunics of fine to medium reticulate fibers. *Prophylls* 2–3, entire, membranous, often red-flushed, obtuse-truncate. *Leaf* solitary, basal, usually slightly shorter than the inflorescence, canaliculate, to 6 mm wide, with slightly thickened hyaline margins. *Bract* leaves to 3 cm long, sheathing at the base only, acuminate. *Spathes* herbaceous, acuminate; inner spathe 3–4.5 cm long, the outer ± half the inner, often with the upper part not sheathing. *Flower* blue; *outer tepals* ca. 3 cm long, lanceolate, the limb ca. 1.5 cm long, spreading to slightly reflexed; *inner tepals* ca. 2 cm long, spreading. *Filaments* ca. 7 mm long, united in the lower third; *anthers* 6 mm long. *Ovary* unusually long, 8–12 mm, enclosed in spathes; style branches ca. 1 cm long, the crests to 8 mm long. *Capsule* and *seeds* not known. Chromosome number not known.

Flowering time: December to January.

Distribution: "Grassland and open *Brachstegia* woodland" in the southern highlands of Tanzania, recorded between Sao Hill and Makumbako, 1,800–2,200 m.—FIG. 2.

Moraea iringensis is closely allied to the more widespread *M. afro-orientale* which occurs in western and central Tanzania, Uganda, western Kenya and the southern Sudan. It differs in being more robust, with larger leaves and flowers, and it is distinctive in having a very long ovary, 8–12 mm long, compared to 3–4 mm in *M. afro-orientale*. In spite of its length, the ovary is almost entirely enclosed in the spathes, in contrast to the exserted ovary found in all allied species.

TANZANIA. SOUTHERN HIGHLANDS: Sao Hill, Iringa district, *Chambers 38* (EAH, K); *Carmichael 331* (EAH); *Robertson 825* (EAH). Kyimbila, Tandala, *Stolz 2362* (K, BM, BR, PRE). Mufindi, *Bjornstad 577* (K). 20 km N of Sunji, Njombe district, *Sturtz 79* (DAR, EAH).

5. **Moraea elliotii** Baker, Handb. Irid. 58. 1892. TYPE: South Africa, Transvaal, marshes near Lake Chrissie, *Scott-Elliot 1592* (K, holotype).

For complete synonymy see Goldblatt (1973).

Plants small to medium, reaching to 55 cm high, usually branched. *Corm* 1.5–2 cm in diameter; tunics of dark brown fairly coarse fibers often extending upwards in a neck. *Prophylls* membranous, becoming dry from above. *Leaf* solitary, terete or linear and canaliculate, inserted near the base or the lower part of the stem, and much exceeding the inflorescence. *Bract leaves* 1–4, 2.5–6 cm long, herbaceous or becoming dry and brown. *Spathes* herbaceous with dry, light brown margins, attenuate; inner spathe 4–6 cm long, the outer ca. 1 cm shorter. *Flowers* blue violet with orange yellow nectar guides; *outer tepals* 2–3 cm long, lanceolate, the limb to 1.5 cm long and 1.2 cm wide, spreading to reflexed at 45°; *inner tepals* 1.5–2.4 cm long, linear-lanceolate. *Filaments* ca. 6 mm long, joined in the lower half; *anthers* ca. 6 mm long. *Style branches* ca. 1 cm long, the crests to 0.5 cm long. *Capsule* ovoid, to 1.2 cm long; *seeds* small, angled. Chromosome number $2n = 12, 24$ (South African collections only).

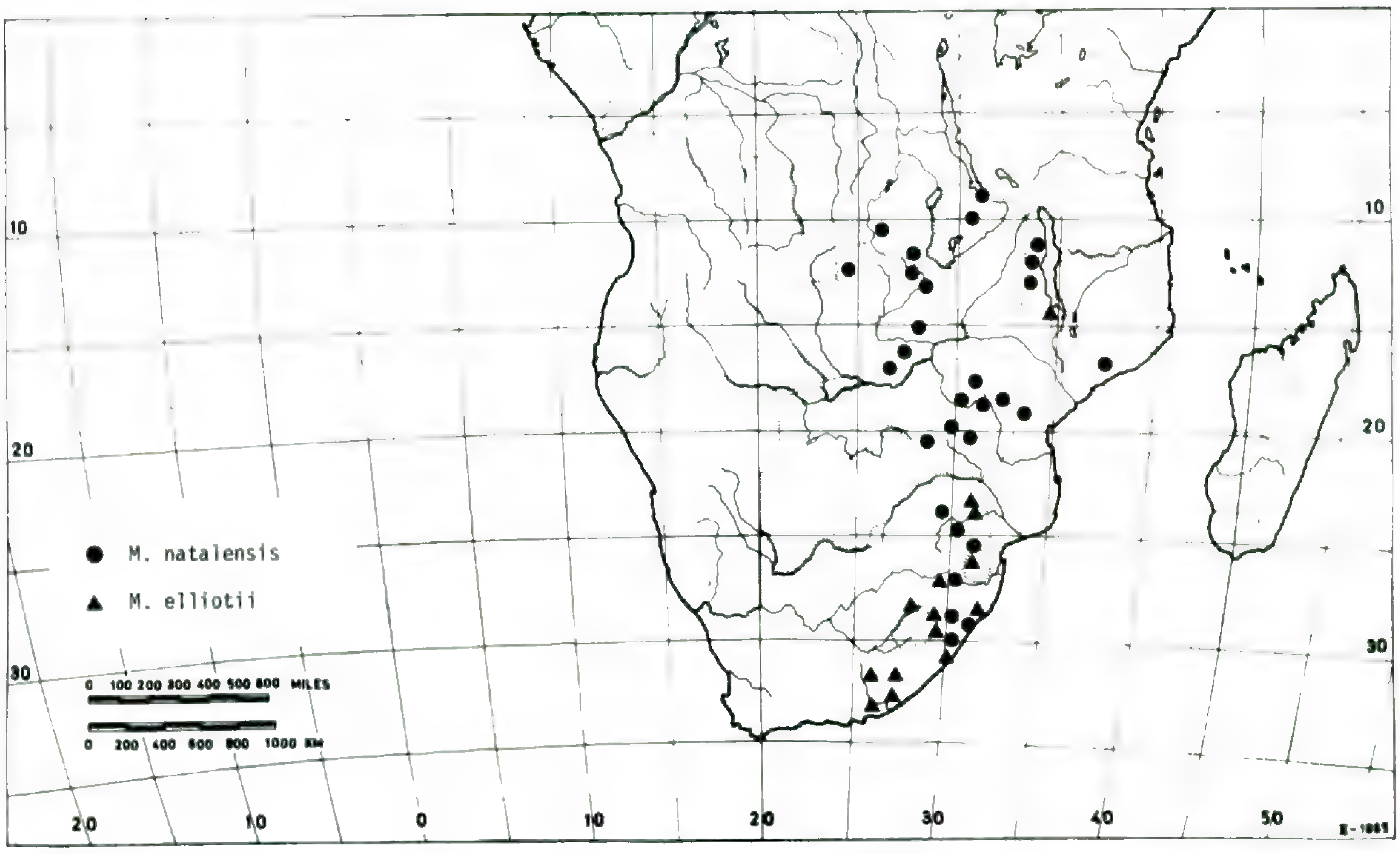

Figure 4. Distribution of *Moraea natalensis* and *M. elliotii*.

Flowering time: September to March.

Distribution: Eastern South Africa, Swaziland, and Malawi.—Fig. 4.

Moraea elliotii is fairly common in the grasslands of South Africa, especially in well-watered highland areas. As defined earlier (Goldblatt, 1973), it includes a wide range of forms, from the early, spring-blooming eastern Cape plants with a ±basal canaliculate leaf, to summer-flowering plants from Natal, Transvaal, and Swaziland, also with a canaliculate leaf, but inserted somewhat above ground level, to terete-leafed, usually late-flowering plants, mainly from the eastern Transvaal. A single collection from Malawi is identical with the latter, and though such a gap in distribution from South Africa to Malawi is unexpected, the Malawian collection must be assigned to *M. elliotii*. The species is clearly predominantly South African, and for further details of synonymy, variation and distribution, readers are referred to my earlier treatment of the species (Goldblatt, 1973).

Moraea elliotii is closely allied to species such as *M. carsonii* from Central Africa and *M. polyanthos* from the southern Cape, and all three species have a similar flower. It would seem more specialized in its solitary leaf and relatively few branches than the multi-leafed and branched *M. polyanthos* and the 2-leafed *M. carsonii*. The more reduced *M. natalensis*, with its short leaf inserted well above the ground and with a somewhat contracted inflorescence, probably evolved from multi-leafed ancestors via plants like *M. elliotii*; and *M. natalensis* is also seen as closely related.

Malawi. central region: Dedza, summit of Ciwan, Chongoni, *Chapman 1176* (SRGH).

6. **Moraea natalensis** Baker, Handb. Irid. 56. 1892. TYPES: South Africa, Natal, *Sanderson 253* (K, lectotype; S, isolectotype); *Sutherland s.n.* (K, paratype).—FIG. 3C.

M. erici-rosenii Fries, Wiss. Ergeb. Schwed.-Rhod.-Kongo Exp., 1911–1912, Bot. Untersuch. 1: 234. 1916. TYPE: Zambia, Kalambo, *Fries 1345* (UPS, holotype; Z, isotype).
M. parviflora N.E. Brown, Trans. Roy. Soc. S. Africa 17: 346. 1929. TYPE: South Africa, Transvaal, Tomson's vlei, Nylstroom, *Pole Evans 19668* (K, holotype; PRE, isotype).

Plants 15–45 cm high, including the leaf, usually branched. *Corm* to 1.5 cm in diameter; tunics of dark brown to black fibers. *Prophylls* membranous with the upper becoming dry from the apex and often lacerated. *Leaf* inserted well above ground, shortly below the inflorescence, canaliculate to terete, to 20 cm long and shortly exceeding the inflorescence or reduced and about as long as the spathes. *Stem* with the lowermost internode very long, and the produced leaf inserted in the upper part. *Bract leaves* if present seldom exceeding 2.5 cm and usually dry and light brown. *Spathes* herbaceous, becoming dry above, the margins dry and pale brown, the apices attenuate; inner spathe 2–3.5 cm long, the outer ca. 1 cm shorter. *Flowers* blue mauve with yellow nectar guides; *outer tepals* 1.4–2 cm long, lanceolate, the limb 0.7–1.4 cm long, up to 1.0 cm wide, reflexed to 45°; *inner tepals* to 1.5 cm long, reflexed. *Filaments* ca. 5 mm long, united in the lower half; *anthers* 4–5 mm long. *Style* branches ca. 6 mm long, the crests to 5 mm long. *Capsule* ovoid-subglobose, 4.5–10 mm long; *seeds* small, angular. Chromosome number $2n = 12$.

Flowering time: November to January (February).

Distribution: Zambia, Malawi, Rhodesia, Mozambique, South Africa; in moist situations, often in vleis and dambos and in seasonal pools.—FIG. 4.

The most striking characteristic of *M. natalensis* is its leaf insertion which is well above ground level at the top of the long lowermost internode. The leaf itself is relatively short, no more than 20 cm long, but more often smaller and sometimes not exceeding the inflorescence spathes. In some forms, notably in the northern part of its range, in Zambia, the stem above the lower internode is much contracted so that the leaf seems to be inserted almost immediately under the inflorescence. In these forms the leaf is often at its shortest, appearing almost bractlike and easily confused with the inflorescence spathes. The type of *M. erici-rosenii* corresponds to this form. Most other collections from Zambia, and Rhodesia, where the species is very common, resemble the typical South African form with a less contracted stem above a longer leaf. The existence of a whole range of forms from the extremely short-leafed, much-contracted type represented by *M. erici-rosenii* to the relatively long-leafed and extended-stemmed type make it necessary to reduce *M. erici-rosenii* to synonymy.

Moraea natalensis is one of the more widespread species in the genus and occupies a similar ecological niche throughout its range. It occupies rather moist depressions or vleis and dambos in open grassland and in exposed rocky situations which are seasonally moist, and is also found around rock pools. It occurs at moderate altitudes of between 1,000 and 2,000 m, though it is also found near the coast in South Africa. It is most closely related to the predominantly

South African species *M. elliotii*, which has a single leaf inserted lower on the stem, usually shortly above the ground.

MALAWI. CENTRAL REGION: Near Tamanda Mission, *Robson 1093* (BM, K, LISC, PRE, SRGH). Kasungu, *Jackson 2299* (K, MAL, PRE, SRGH). Kasungu National Park, *Hall-Martin 1364* (SRGH). NORTHERN REGION: S. Vipya, Lwanjati Peak, *Pawek 8905* (SRGH, MO).

MOZAMBIQUE. MANICA & SOFALA: 12 km from Vila Pery, *Torre & Correia 13180* (LISC). ZAMBEZIA: Mujeba, on Pibane road, Quelimane district, *Faulkner K152* (BR, K, PRE, S).

RHODESIA. CENTRAL REGION: Marandellas, *Dehn 556* (SRGH); *Rattray 829* (SRGH); *Day s.n.* (SRGH-2129); *Collins 10* (K, SRGH). Rusape, *Hopkins s.n.* (SRGH-6830); *Munch 455* (K, SRGH). Salisbury, *Eyles 1896* (K, PRE, SAM), *3737* (SAM, SRGH), *6099* (BOL, K, SRGH); *Willoughby s.n.* (SRGH). Surprise siding, Selukwe, *Taylor s.n.* (SRGH-2625). Near Que Que, *Bingham 374* (K, SRGH). Gwelo, *Loveridge 540* (K, PRE, SRGH). Darwendale, *Gordon 193017* (K, SRGH). SOUTHERN REGION: Near Fort Victoria, *Plowes 3154* (K, LISC, PRE, SRGH). WESTERN REGION: Bulawayo, *Brain s.n.* (SRGH). Matobo district, *Miller 1998* (K, LISC, MO, PRE, SRGH), *2051* (MO, PRE, SRGH). Matopos, *Borle 58* (K); *Garley 112* (K, SRGH); *Eyles 1144* (ISRGH). Lochview, *Cross 335* (SRGH).

ZAÏRE. SHABA: Lumbumbashi (Elisabethville), *Hock s.n.* (BR). Near Mukumbi, *Hoffmann 962* (BR).

ZAMBIA. CENTRAL REGION: Lusaka, *King s.n.* (K); *Best 4, 10* (K), *82* (SRGH). NORTHERN REGION: Mbala (Abercorn) district, Kalambo Falls, *Richards 19295* (K). 25 km W of Kasama, *Robinson s.n.* (K). SOUTHERN REGION: Machipapa, Mazabuka district, *White 6253* (K). Katomo, Batoka Plateau, *Sykes 267* (K). Kaloma, *Fanshawe 9179* (SRGH); *Mitchell 17/29* (SRGH). Between Chomo and Monze, *van Rensburg 3084* (BM, K, SRGH). Chomo, *Astle 1841* (SRGH); *Lawton 1185* (K, SRGH). WESTERN REGION: Kalenda dambo, Mwinilunga district, *Milne-Redhead 3597* (BR, K, PRE). Zambezi Rapids, Mwinilunga district, *Richards 17146* (K, SRGH); *Lewis 6224* (K, MO). Kitwe, dambo, *Linley 35* (MO, SRGH). Nchanga, *Ferrar s.n.* (SRGH-4800).

7. **Moraea thomsonii** Baker, Handb. Irid. 57. 1892; Bot. Mag. *tab. 7976.* 1904. TYPE: Tanzania, "plateau north of Lake Nyassa," Oct. 1880, *Thomson s.n.* (K, holotype).—FIG. 5.

M. stricta Baker, Vierteljahrsschr. Naturf. Ges. Zürich 49: 178. 1904. TYPE: South Africa, Transvaal, Shilouvane, *Junod 563* (Z, holotype; K, LD, isotypes).
M. tellinii Chiov., Ann. Bot. (Rome) 9: 138. 1911. TYPE: Ethiopia, Begemdir & Simen, Debarek, *Chiovenda 3007* (F, lectotype); several other types cited, all from Ethiopia.
M. curtisae Foster, Contr. Gray Herb. 127: 46. 1939. TYPE: Kenya, Norok, Noyrosera, 60 km SE of Narok, *Curtis 676* (GH, holotype).
M. trita N. E. Brown, Trans. Roy. Soc. S. Africa 17: 347. 1929. TYPE: South Africa, Transvaal, Lydenburg, *Wilms 1419* (K, holotype; P, PRE, isotypes).
M. parva N. E. Brown, Trans. Roy. Soc. S. Africa 17: 347. 1929. TYPE: South Africa, Transvaal, Woodbush, *Moss 15564* (K, holotype).
M. mossii N. E. Brown, Trans. Roy. Soc. S. Africa 17: 347. 1929. TYPE: South Africa, Transvaal, Johannesburg, *Moss 15805* (K, holotype; PRE, isotype)

Plants small, 12–30 cm high, branched, leafless when in flower. *Corm* 1–2 cm in diameter; tunics dark brown, of tough reticulate fibers. *Prophylls* dry and irregularly broken. *Leaf* solitary, quite dry, or lacking at flowering time, occasionally a new leaf emergent and then not attached to the flowering stem, slender, terete, long and trailing. *Branches* short to ±sessile, subtended by dry bract leaves. *Spathes* usually quite dry and papery at flowering, acuminate, becoming lacerated with age; inner spathe 2.5–4 cm long, the outer 5–10 mm shorter. *Flower* pale blue lilac with yellow orange nectar guides; *outer tepals* 1.5–2 cm long, lanceolate, the limb to 1 cm, spreading; *inner tepals* 1.4–1.7 cm long, erect, becoming outspread. *Filaments* 4–5 mm long, free in the upper third; *anthers*

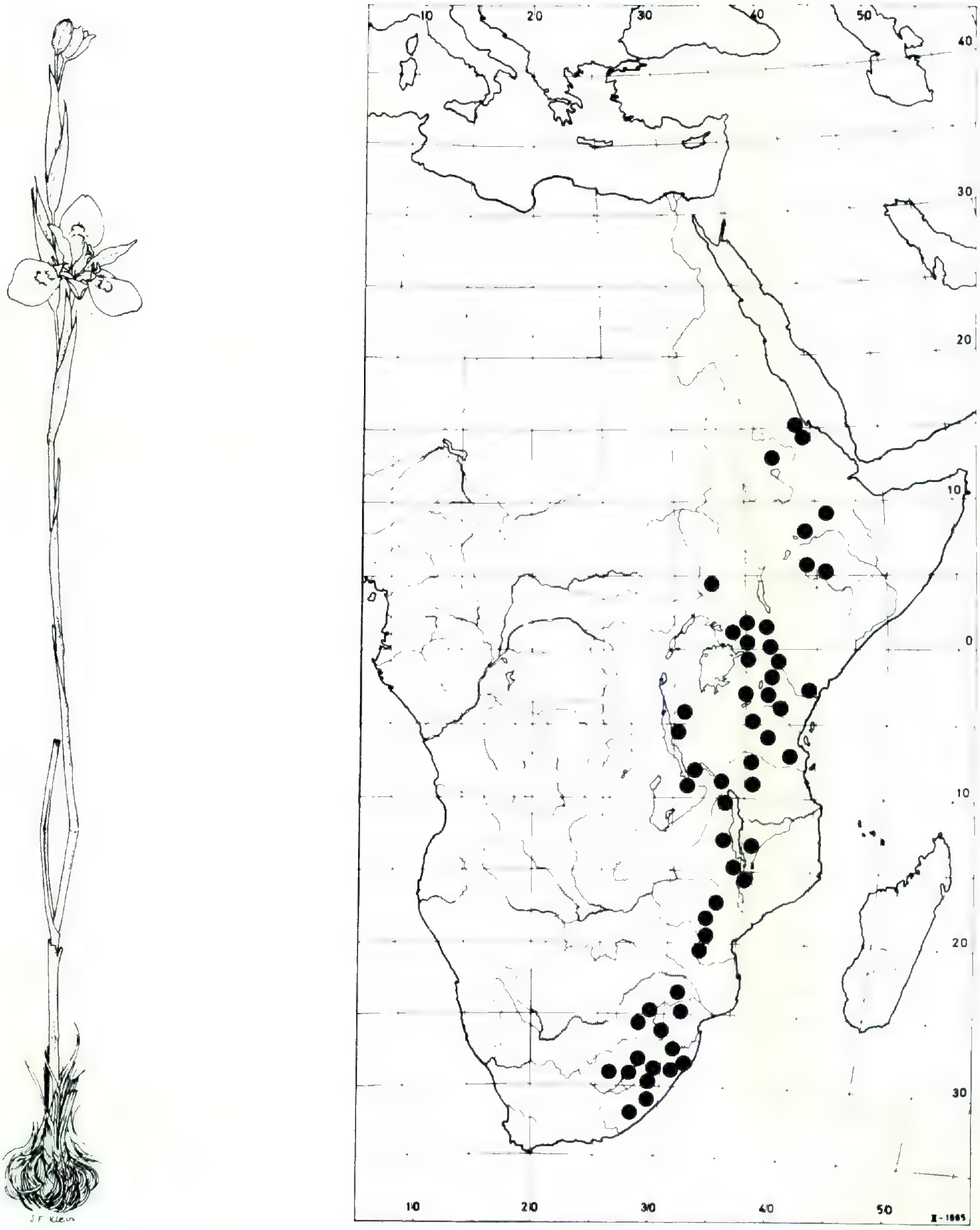

FIGURE 5. Morphology and distribution of *Moraea thomsonii* (×0.5).

4–5 mm long. *Style branches* 7 mm long, the crest vestigial or 3–5 mm long. *Capsule* ovoid, ca. 1 cm long; *seeds* small, angular. Chromosome number $2n = 12$, 24, 36, 48.

Flowering time: (August) September to November (December) south of the equator, December to June (August) north of the equator, in the dry season before the rains begin.

Distribution: Widespread, in dry grassland in the eastern half of Africa; extending from the summer rainfall areas of South Africa through Mozambique, Rhodesia, Malawi, and eastern Zambia to Tanzania, Uganda, Kenya and Ethiopia. —FIG. 5.

Several species are reduced here to synonymy in *M. thomsonii*, notably *M. tellinii* from Ethiopia, *M. curtisiae* from Kenya, and *M. stricta* from South Africa. These all differ to a small extent from *M. thomsonii*, but they have its characteristic growth habit and peculiar terete leaf, characters which are considered more significant taxonomically than the minor floral differences that are perhaps to be expected in such a widely distributed species.

The typical form of *M. thomsonii* which occurs in Malawi and adjacent Zambia and Tanzania has short, almost vestigial style crests, but has relatively broad tepals and style branches. Plants occurring further to the north and also to the south have well-developed style crests. The northern forms, however, have the broad tepals and style branches of the type, while the South African form, earlier treated as *M. stricta* by me (Goldblatt, 1973), has rather narrow tepals and style branches. Plants occurring in Rhodesia are intermediate between the typical and southern forms and usually have style crests.

Moraea thomsonii is one of the more widespread species in the genus, extending almost the length of the eastern half of Africa, from the eastern Cape Province of South Africa to northern Ethiopia. It occurs in open grassland and typically flowers towards the end of the dry season. The leaf and flowering stem are produced at different times, the long, terete leaf emerging after the first rains, and attaining full size during the wet season. The leaf dies back in the dry season, often becoming broken and decayed by the time the stem and, subsequently, the flowers are produced. Owing to the widespread practice in Africa of burning grasslands at the end of the dry season, the leaf of *M. thomsonii* is often charred or is entirely destroyed, so that flowering specimens frequently lack leaves.

Moraea thomsonii is generally easy to recognize in the herbarium because specimens usually lack leaves, or if these are present, it is obvious that the leaf was dead when collected. Difficulty is sometimes experienced in deciding if the leaf was in fact dry when gathered and then the terete nature of the leaf, the short, often sessile branches and dry, almost transparent spathes are sufficient for determination.

ETHIOPIA. ARUSI: Mt. Chillalo, *Scott s.n.* (K). BEGEMDIR & SIMEN: Debarek, Amhara, *Chiovenda 3007* (F). ERITREA: Hamasen, *Fiori 895* (F). Near Adi Nefas, Hamasan, *Pappi 4149* (F). Amba-Dero, *Pappi 3541* (F). Belesa, Hamasen, *Terraciano & Pappi 343* (F). At Taclesan, *Terraciano & Pappi 415* (F). HARAR: Mt. Achim, *Bally 10054* (EAH, K). SIDAMO: 15 km SE of Meghelli, *Burger 1827* (F, K). Mogada forest, *Mooney 5469* (K). Wadera, *Mooney 5629* (EAH, F, K). 15 km S of Adola, *Bally 3137* (K). Agheremeriam, *Gillett 14549* (BR, EAH, F, K). Between Neghelli and Filtu, *de Wilde 6675* (WAG).

KENYA. COAST PROVINCE: District around Nyora, *Routledge 1908* (K). CENTRAL PROVINCE: Nairobi National Park, *Verdcourt 3284* (K). Between Ngong and Kikuyu, *van Someren 1437* (EAH, K). Nanyuki, *Watt s.n.* (K). RIFT VALLEY PROVINCE: Elgeyo, *Battiscombe 1184* (EAH, K). Kaptagat, *Agnew & Agnew 9031* (MO); *Verdcourt 2148* (EAH, K, PRE). Kapiyet, *Dauglish 82* (K). Trans Nzoia, *Tweedie 443* (K). Mt. Elgon, *Lugard 548* (K). Kitale, *Thorold 2752* (K). NORTHERN FRONTIER: Near Kisima, *Leakey 8544* (K). NYANZA PROVINCE: Tinderet, *Poviano s.n.* (F). SOUTHERN PROVINCE: Near Kongoni River, *Fries & Fries 1538* (K, S, UPS). 60 km SE of Narok, Noyrosera, *Curtis 676* (GH).

MALAWI. NORTHERN REGION: Nyika National Park, *Pawek 1390* (SRGH). Nyika Plateau, *Robson 231* (K, LISS, SRGH). CENTRAL PROVINCE: Between Dedza and Ncheu, *Jackson 148* (K). Clintembwe, Kota Kota district, *Brass 17579* (K, MO). SOUTHERN REGION: Mlanje Mt., *Burtt Davy 21981* (K); *Pawek 3795* (K). Zomba Mt., *Salubeni 89* (MAL, SRGH). Mt. Malosa, *Whyte s.n.* (K).

MOZAMBIQUE. MANICA & SOFALA: Báruè, Serre de Choa, *Mendonça 301* (LISC). Between Skeleton Pass and Chimanimani Plateau, *Grosvenor 225* (LISC, SRGH). NIASSA: Namiamba, near Vila Cabral, *Mendonça 776* (LISC).

RHODESIA. EASTERN REGION: Chimanimani Mts., *Munch 325, 326* (SRGH). The Corner, Chimanimani Mts., *Wild 3350* (K, SRGH); *Sturgeon s.n.* (SRGH-30671, K, LISC, PRE); *Chase 2973* (BM, MO, SRGH). Melsetter, *Plowes 2460* (SRGH), *2800* (LISC, SRGH). Banti North, Umtali, *Chase 7828* (SRGH). Inyanga, *Leach 8139* (K, SRGH). Mare River, Inyanga, *Wild 3859* (K, MO, SRGH). Slopes of Rukotso, Inyanga, *Phipps 734* (SRGH). S of Pungwe View, *Methuen 309* (K).

SUDAN. EQUATORIA: (reported as Uganda) Imatong Mts., *Eggeling 3558* (K).

TANZANIA. CENTRAL PROVINCE: Wotta, Mpwapwa district, *Gane 133* (EAH, K). EASTERN PROVINCE: Morogoro, *Schlieben 1237* (BR, K). NORTHERN PROVINCE: Ngorongoro, *Tanner 3863* (K). Liliondo, Masailand, *Fosbrooke 20* (K); *Gibbins s.n.* (K). W slopes of Kiliamanjaro, *Greenway 6704* (K, PRE). Hanang Mt., *Burtt 4010* (K); *Geilinger 1313* (K, Z). Mpololo, Moshi district, *Haarer 1478* (K). Oldeani Volcano, *Burtt 4232* (K). SOUTHERN HIGHLANDS: Ruhudje-Lupembe, *Schlieben 1237* (K, LISC, MO, PRE). Iringa district, *Greenway 3429* (EAH, K). Mbeya Mt., *Geilinger 2797* (K,Z). WESTERN PROVINCE: Heru, Kasulu district, *Eggeling 6195* (BR, EAH, K). S of Sisaga, Kigoma district, *Jefford & Newbold 1770* (K). Keto Mt., 15 km from Zambia border, *Richards 6186* (K).

UGANDA. Without precise locality, *Bally 10748* (K). NORTHERN PROVINCE: Mt. Debasien, *Eggeling 2693* (K).

ZAMBIA: EASTERN REGION: Lundazi, Nyika Plateau, *Pawek 2854* (K, MAL). NORTHERN REGION: Lumi marsh, Kawimbi, *Richards 6116* (K).

Subgenus GRANDIFLORA Goldbl.

8. **Moraea spathulata** (L.f.) Klatt in Th. Durand & Schinz, Consp. Fl. Afr. 5: 152. 1895.—FIG. 7A.

Iris spathulata L.f., Suppl. Pl. 99. 1781. TYPE: South Africa, Cape, Langkloof, Wolwekraal, *Thunberg s.n.* (Herb. Thunberg 1172, UPS, holotype).
I. spathacea Thunb., Diss. Iride no. 23. 1782. TYPE: as for *I. spathulata* L.f.
Moraea spathacea (Thunb.) Ker, Bot. Mag. *tab. 1103.* 1808, non Thunb., 1787.
M. longispatha Klatt, Linnaea 34: 560. 1866. TYPE: South Africa, Cape, Transkei, banks of Kei River ("Tambikuland"), *Ecklon & Zeyher Irid. 3* (MO, lectotype).
M. spathulata subsp. *transvaalensis* Goldbl., Ann. Missouri Bot. Gard. 60: 253. 1973. TYPE: South Africa, Transvaal, near Sabie, *Goldblatt 610* (BOL, holotype; MO, isotype).
M. spathulata subsp. *saxosa* Goldbl., Ann. Missouri Bot. Gard. 60: 254. 1973. TYPE: South Africa, Transvaal, summit of Long Tom Pass, *Goldblatt 612* (BOL, holotype; PRE, isotype).
M. spathulata subsp. *autumnalis* Goldbl., Ann. Missouri Bot. Gard. 60: 254. 1973. TYPE: South Africa, Cape, Transkei, Nyameni Mouth, Port Edward district, *Strey 8619* (PRE, holotype; NH, isotype).

Plants large, 50–90 cm high, solitary or in small clumps. *Corm* 1.5–2 cm in diameter; tunics of brown, finely reticulated fibers. *Prophylls* prominent, brown to pale, firm in texture, brittle, dry, entire or irregularly broken, or frayed at the apex. *Leaf* solitary, flat or canaliculate, to 1.5 cm wide. *Stem* simple or occasionally bearing one branch. *Bract leaves* 2–3, often dry and brown, to 15 cm long, rarely overlapping. *Spathes* herbaceous, or becoming dry and brown from the apex, attenuate; inner spathe 10–14 cm long, outer ca. ¾ the inner. *Flower* pale yellow; *outer tepals* 3.5–5.5 cm long, the limb 2–3.5 cm, spreading; *inner tepals* 3–4 cm long, erect. *Filaments* 8–12 mm long, free in the upper third;

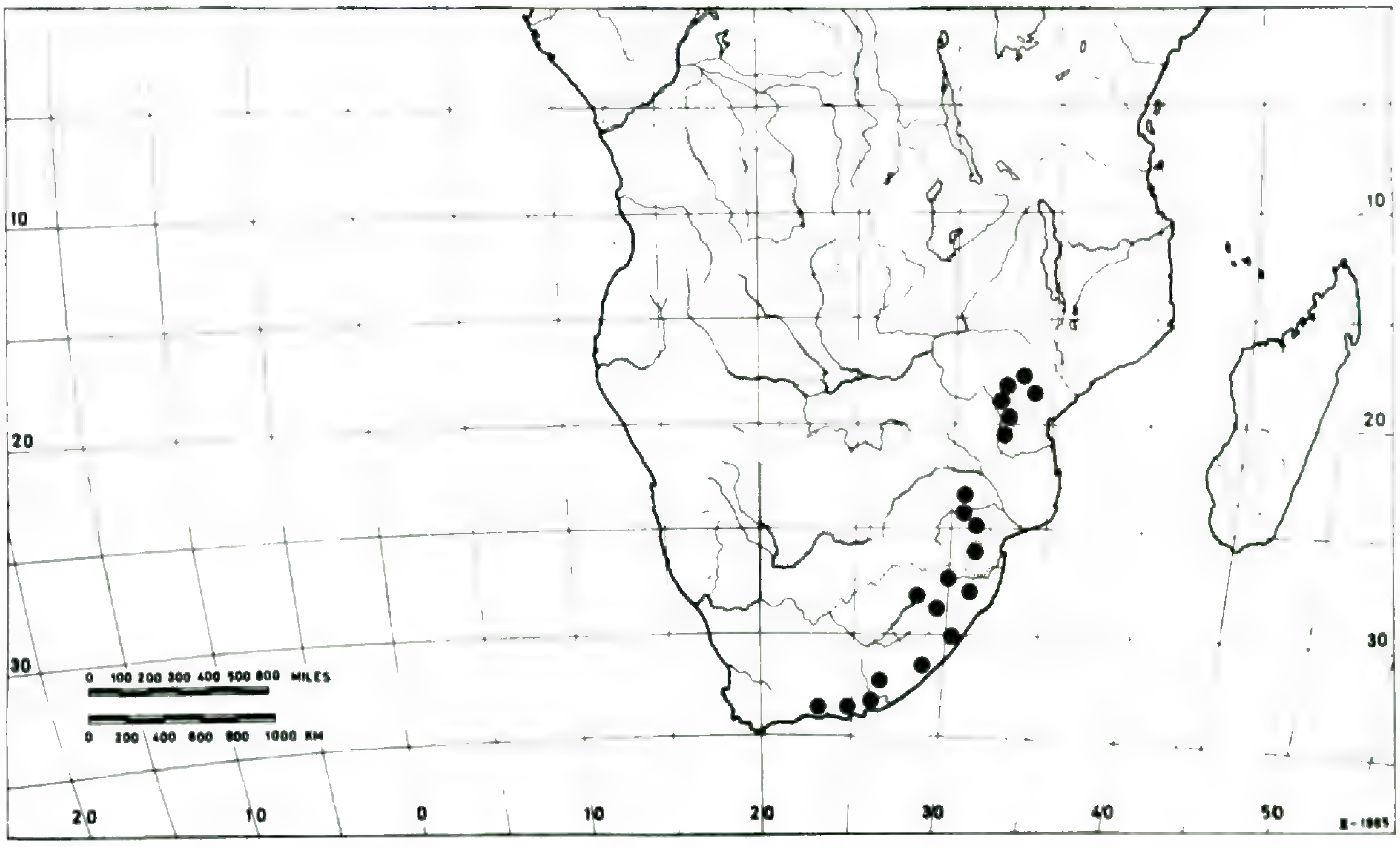

FIGURE 6. Distribution of *Moraea spathulata*.

anthers 8–12 mm long. *Ovary* 2–3 cm long; style branches 1.2–1.8 cm long, the crests to 1 cm long. *Capsule* 3.5–5.5 cm long; *seeds* large, flattened. Chromosome number $2n = 12$ (South African plants only).

Flowering time: (November) December to March (early April).

Distribution: Open grassland in the Inyanga and Chimanimani highlands of Rhodesia and Mozambique, also in South Africa, Lesotho, and Swaziland.—FIG. 6.

The tall, summer-flowering *Moraea* frequently collected in the Chimanimani and Inyanga highlands of Rhodesia and Mozambique is clearly closely allied to the *M. spathulata* complex of South Africa. The plants from the Chimanimanis in particular are virtually identical to the Transvaal and Swaziland forms which I previously referred to *M. spathulata* subsp. *saxosa* Goldbl. (Goldblatt, 1973). Since 1973 when I recognized *M. spathulata* as comprising four subspecies, I have had the opportunity to observe living plants in several places and to see more herbarium material. As a result, it has become clear that my attempt to subdivide *M. spathulata* was not satisfactory, and the proposed subspecies did not accurately reflect the variation found in the species. The subspecies *autumnalis* from the Transkei is merely a very early blooming coastal form and must be included in the typical form. *Moraea spathulata* in the southern part of its range in the Knysna district of the Cape Province blooms from July to September but not unusually in June or even May, thus the March to May blooming subsp. *autumnalis* is not particularly unusual. The remaining two subspecies, subsp. *transvaalensis* and subsp. *saxosa*, both from the Transvaal and Swaziland, differ from one another mainly in that the lower-altitude subsp. *transvaalensis*

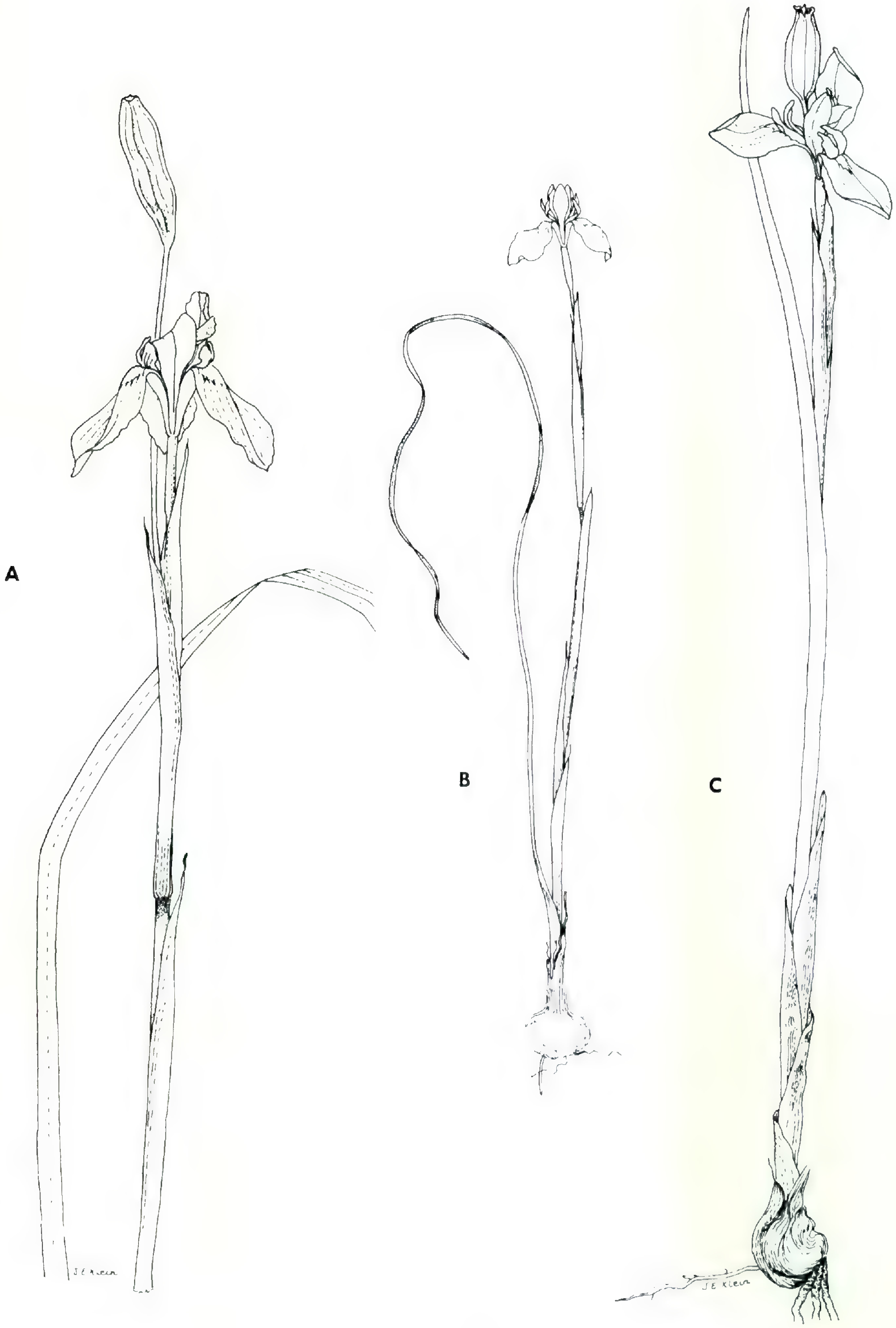

FIGURE 7. *Moraea* species.—A. *M. spathulata*.—B. *M. inyangani*.—C. *M. schimperi* (×0.5).

forms clumps, while the higher-altitude subsp. *saxosa* appears to be predominantly solitary in habit and has a slightly longer ovary and capsule. However, when the entire pattern of variation in *M. spathulata* is considered, both the tendency to solitary habit, and the longer ovary of subsp. *saxosa* and the features of subsp. *transvaalensis* now seem altogether too insignificant to make any taxonomic recognition worthwhile. It seems far more useful to recognize *M. spathulata* as a single, complex, and variable entity.

North of the Limpopo River *M. spathulata* thus extends as far as the Inyanga region of Rhodesia-Mozambique. The largest forms occur in Inyanga, some plants even bearing branches while rather dwarfed forms occur in the Chimanimanis. Differences between the two appear significant until the few collections from the intervening highland areas in Mozambique are considered, and these prove intermediate in all characteristics.

MOZAMBIQUE. MANICA & SOFALA: Tsetserra, *Exell, Mendonça & Wild 332* (LISC); *Torre & Correia 15687* (LISC). Gorongosa Mts., summit, *Tinley 2436* (SRGH). Serra Messambuzi, *Torre & Correia 13302* (LISC). Between Mussapa River and frontier at Tendera, *Torre & Correia 13159* (LISC). Báruè, Serra de Choa, *Torre & Correia 15485* (LISC).

RHODESIA. EASTERN REGION: Melsetter, *Hanmer s.n.* (SRGH-18354); *Chase 1421* (BM, K, SRGH). Melsetter district, Mutsarara farm, *Crook 318* (SRGH). Glendingwe Estate, *Plowes 3477* (SRGH). Pork Pie Hill near Melsetter, *Bamps, Symoens & van den Berghen 776* (BR, SRGH). Inyanga, *Chase 4351* (BM, K). Inyangani Mt., *Chase 8124* (BM, K, LISC, PRE, SRGH); *Plowes 2429* (SRGH); *Whellan & Davies 984* (K, SRGH); *Fries, Nrolindh & Weimarck 4967* (BM, BR, PRE). Mt. Gungingurwe, Stapleford, *Wild 5711* (K, MO, PRE, SRGH). Bant North, Umtali district, *Wild 4522* (K, LISC, MO, PRE, SRGH). Himalayas-Engwa, *Wild 4456* (K, LISC, SRGH). Vumba Mts. near Umtali, *Obermeyer 2113* (PRE).

9. **Moraea schimperi** (Hochst.) Pic.-Serm, Webbia 7: 349. 1950.—FIG. 7C.

Hymenostigma schimperi Hochst., Flora 27: 24. 1844. TYPE: Ethiopia, Begemdir & Simen "Enschedcap," *Schimper 1173* (B, holotype; BM, F, K, M, MO, P, S, isotypes).
H. tridentatum Hochst., Flora 27: 25. 1844. TYPE: Ethiopia, Begemdir & Simen, Barnam, Mt. Bachit, *Schimper 1296* (K, lectotype).
Vieusseuxia schimperi (Hochst.) A. Rich., Tent. Fl. Abyss. 2: 305. 1850 (Hist. Nat. Bot. v. 5).
V. tridentata (Hochst.) A. Rich., Tent. Fl. Abyss. 2: 305. 1850.
Iris diversifolia Steud., m.s. (cf. A. Rich., Tent. Fl. Abyss. 2: 305. 1850).
Xiphion diversifolium Steud. ex Klatt, Linnaea 34: 572. 1866, nom. illeg. superfl. TYPE: as for *Hymenostigma schimperi* Hochst.
Moraea diversifolia (Steud. ex Klatt) Baker, J. Linn. Soc., Bot. 16: 130. 1877.
M. welwitschii Baker, Trans. Linn. Soc. London, Bot., Ser. 2, 1: 270. 1878. TYPE: Angola, Huila, Lopollo River, *Welwitsch 1548* (BM, holotype; K, LISU, P, isotypes).
M. zambeziaca Baker, Fl. Trop. Afr. 7: 340. 1898. TYPE: Zambia, Mangaja hills, *Meller s.n.* (K, holotype).
M. hockii De Wild., Repert. Spec. Nov. Regni Veg. 11: 540. 1913. TYPE: Zaïre, Shaba, between Buggege and Lukoni, *Hock s.n.* (BR, holotype).

Plants 20–40 cm high, unbranched. *Corm* 1.5–2 cm in diameter; tunics brown, fibrous. *Prophylls* 3–5, large and prominent, entire, firm, usually dark brown. *Leaf* solitary, basal, canaliculate to flattened, 9.6–15 mm wide, emerging as flowering begins, but eventually much exceeding the inflorescence. *Stem* usually short at flowering time but elongating in fruit. *Bract leaf* usually solitary, 10–15 cm long, becoming dry and brown. *Spathes* usually dry and brown, (6–)7–10 (–12) cm long; outer spathe about ¾ the length of the inner. *Flower* blue purple with yellow white nectar guides; *outer tepals* lanceolate, 4–6.5 cm long, the limb

equal to or slightly exceeding the claw; *inner tepals* erect, 3.5–4.5 cm long. *Filaments* 9–15 mm long, united in the lower half; *anthers* 8–12 mm long. *Ovary* 1.5–2 cm long; style branches 1.5–2 cm long, the crests 1–2 cm long. *Capsule* 2.5–3.5 cm long; *seeds* flattened and ±discoid. Chromosome number $2n = 12$.

Flowering time: From the end of the dry season into the early wet season, August to November (December) south of the equator; November to May, occasionally until July in West Africa and Ethiopia.

Distribution: Widespread from Rhodesia north and west through Central and East Africa, to Angola, Zambia, Malawi, Mozambique, Tanzania, Zaïre, Burundi, Sudan, Ethiopia, Cameroons and Nigeria; often in marshy or wet situations, occasionally in grassland.—Fig. 8.

Moraea schimperi has been given a surprising number of names which seems remarkable in the light of its singular morphology and habit. This is probably explained more by its great geographic range than by any morphological differences, and in fact most of its synonyms have been applied to plants from different areas of Africa. *Moraea schimperi* extends from the Rhodesian-Mozambique highlands in the south, west to Angola and north, through Zaïre and Burundi to southern Sudan and Ethiopia. It also occurs in the higher areas of Nigeria and Cameroons, with a large break in the range over the Congo Basin. Significantly it is also absent from Uganda and Kenya, where the highlands may be of too recent origin for it to have become established.

Moraea schimperi usually occurs near a permanent water source, either underground or at the surface, in a vlei or dambo, or along a stream, but is also found in well-drained grassland in areas of high rainfall. It flowers at the end of the dry season and continues in bloom in the early wet season. Thus in the southern tropics it blooms from September through October and into November and early December. On the equator and to the north, plants most often begin flowering in December to February, and continue into March and May. The morphology of *M. schimperi* is most distinctive. The flowering stem appears before or as the new season's leaf emerges, and early in the season the bright blue flowers are borne well above the leaf apex. The prophylls, bracts, and spathes are large, and their usually rich brown color is alone sufficiently characteristic to permit determination. As the season progresses, stem and leaf continue to grow, and by the time the seeds are ripe the stem may be a meter high and the leaf much longer. There is only a small degree of variation from this pattern, notably in plant size, with forms from Nigeria-Cameroons and also some in Ethiopia being more slender than the comparatively robust plants in the southern part of its range.

Though clearly related to the *M. spathulata* complex, as can be seen from the similarity of the bracts and prophylls, *M. schimperi* is unusual in this alliance in having blue purple flowers. The treatment of *M. schimperi* here differs somewhat from that of Geerinck (1970) in that *M. arnoldiana* is not considered a synonym. The latter is a late-blooming species from Zaïre and is assigned to synonymy under *M. macrantha* in this treatment.

Angola. bie: Chitembo, *Barbosa & Moreno 12245* (LISC). cuanza sul: *Murta & Silva 857* (COI, LISC). huambo: Rio Cuanza, Mucosa, *Monteiro & Murta 1884* (COI,

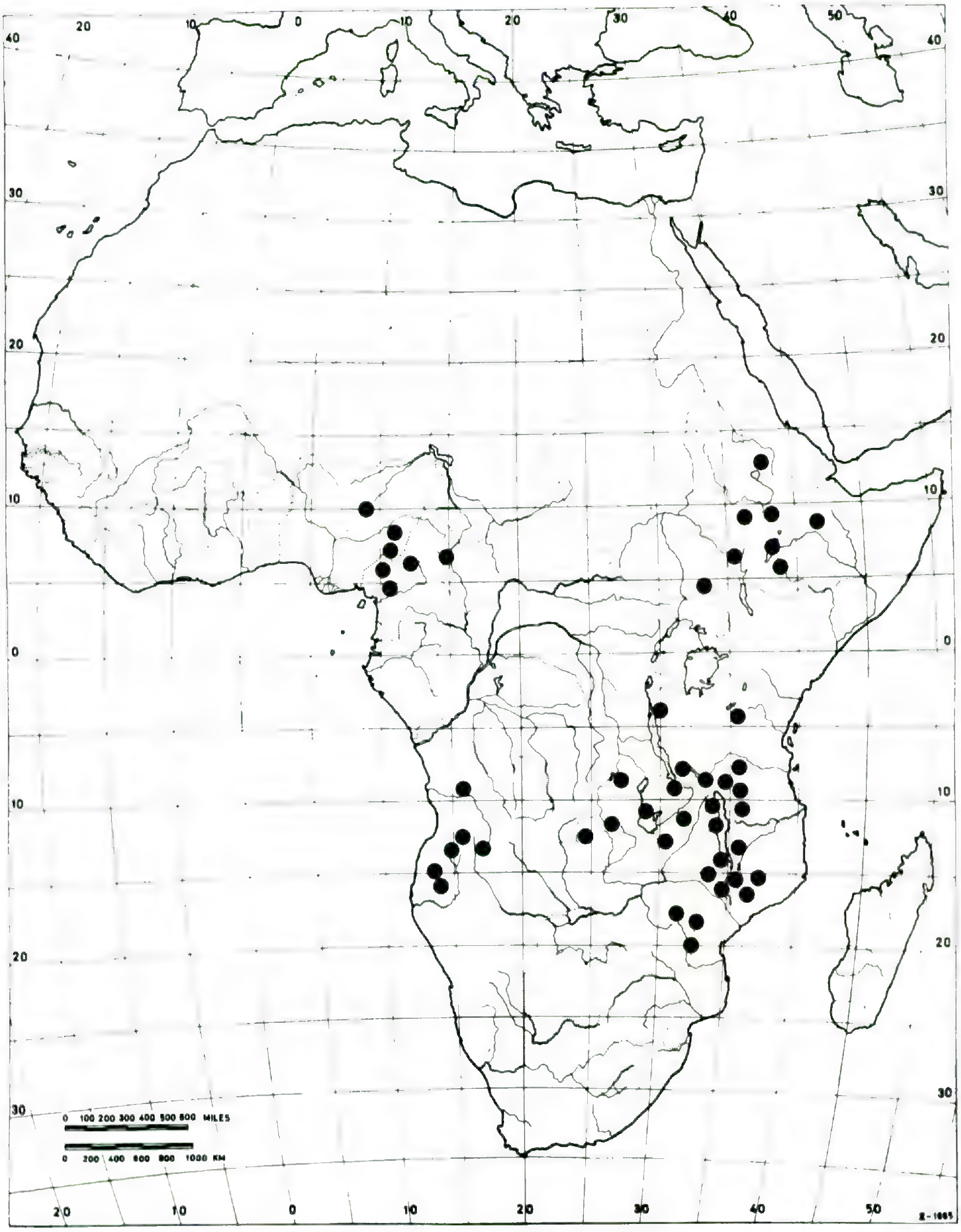

Figure 8. Distribution of *Moraea schimperi*.

LISC, SRGH). Huambo (Nova Lisboa), *da Silva 3188* (LISC, PRE). huila: Missae Catolica, Huila, *Santos 62* (LISC). Lopollo River, *Welwitsch 1548* (BM, COI, K, LISU, P). Near Vila Arture de Paiva, *Leach & Cannell 13861* (K, LISC). Lubango (Sa de Baneira), Rio Caia, *Henriques & Brites 1137* (K, LISC, LISU, PRE). Humpata, *Mendes 1816* (LISC). Cheila Mts., *Gosseiler 13316, 13317* (LISC). malanje: *Gossweiler 922* (P).

Burundi. Bururi, *Becquet 162* (BR, EAH, K, WAG); *Reekmans 1041* (BR, EAH). Near Kumuyange, *Lewalle 6131* (BR, MO).

Cameroon. west: *Bauer 22* (K). Bamenda, 4 km NE of Bambili, *Bauer 154* (K). Between Bamenda and Santa, *Keay s.n.* (FHI-28348, K, P). east: Nganha Mts., E. Ngoaun-

déré, *Jacques-Felix 8632* (P); *de Wilde 4521* (WAG). E of Ngoaundéré, *Raynal & Raynal 12236* (P); *de Wilde 4312* (WAG). Dschang, Mt. Bamboutos, *Villiers 672* (P); *Jacques-Felix 2707* (P); *Saxer 88* (K, WAG, Z). Dschang, *Meurillon 765* (BR). Djuttitsa, *Meurillon 179* (BR), *745* (P), *1212* (BR, K, P). Mt. Santa, *Jacques-Felix 2810* (P). Gotel Mts., NNE Banyo, *Letouzey 8592* (P).

ETHIOPIA. ARUSI: Between Shashamane and Dodollo, *de Wilde 6823* (WAG). Near Asela, *de Wilde 6595* (MO, WAG). Near Kofole, *Mooney 7106* (F, K, S). Between Bekoji and Adaba, *Gilbert 1150A* (K). BEGEMDIR & SIMEN: Near Michubbi, *Pichi-Sermolli 2674* (F, K). "Enschedcap," *Schimper 1173* (B, BM, F, K, M, MO, P, S). Sering, *Schimper 1536, 1537* (P). HARAR: Gara Mullata Mts., *Gillett 5332* (EAH, F, K, P, S); *Burger 1706* (K), *2933* (F, K); *de Wilde 6335* (WAG). SHOA: *Negri 413* (F). Between Addis Ababa and the Blue Nile, *Buscalioni 957* (F). Mt. Zuguola, *Buscalioni 2158* (F). SIDAMO: S of Agere Selam, *de Wilde 6721* (WAG). SE of Agere Selam, *de Wilde 10298* (MO, PRE, WAG). WOLEGA: Bari, *Smeds 1241* (K). N of Beica, *Mooney 7729* (EAH, K).

MALAWI. NORTHERN REGION: Chelinda Bridge, Nyika, *Pawek 1407* (SRGH). Nyika Plateau, *Cottrell 3, 65* (SRGH); *Robson 326* (BM, BR, K, LISC, SRGH). Mzuzu, Marymount, *Pawek 5833* (MO, SRGH). Vipya Mts., *Chapman 1702* (K, LISC, SRGH); *Garley 576* (SRGH). CENTRAL PROVINCE: Dedza, *Brass 17632* (K, MO, SRGH); *Kulumule 2* (K, SRGH). Chongoni Forest Reserve, Dedza district, *Salubeni 829* (MAL). SOUTHERN PROVINCE: Chambe Plateau, Mt. Mulanje, *Newman & Whitmore 653* (BR, K, SRGH, WAG). Mt. Mulanje, *Forbes 67* (EAH); *Greenway 6306* (EAH, PRE). Lichenya Plateau, Mulanje Mts., *Pawek 3793* (MAL). Limbe, off Cholo road, *Moriarty 399* (MAL).

MOZAMBIQUE. NIASSA: Amaramba near Mandimba, *Mendonça 666* (LISC). TETE: Between Furancungo and Angonia, *Torre 3362* (LISC). ZAMBEZIA: Namuli hills, *Last s.n.* (K). Near Gurué, *Torre & Correia 15923* (LISC). Serra de Gurué, *Mendonça 2229* (LISC).

NIGERIA. NORTHERN REGION: Vom, Jos Plateau, *Dent Young 245* (K); *McClintock 199* (K). Mambila Plateau, *Tuley 1929* (K); *Latilo & Daramola s.n.* (FHI-34380, BR, K, S, WAG); *Wit, Gbile & Daramola 2076* (FHI); *Hepper 1774* (BR, K, P); *Gbile & Daramola s.n.* (FHI-62880, WAG). Between Nguroje and Maisamari, *Chapman 2640* (FHI). Vogel Peak, *Hepper 1504* (K, P).

RHODESIA. EASTERN REGION: Melsetter, Markhams Kloof, *Crook M151* (K, LISC, MO, PRE, SRGH). Inyanga downs, *Drewe 18* (SRGH). CENTRAL REGION: Salisbury, *Eyles 1791* (K, PRE, SAM, SRGH). Cleveland Dam, *Wild 3871* (K, SRGH). Marandellas, *Rattray 562, 309* (BM, SRGH); *Corby 196* (SRGH).

SUDAN. EQUATORIA: Imatong Mts., *Andrews 1895* (K); *Johnston 1492* (K); *MacDonald 80* (BM). Kippi, *Chipp 89* (K).

TANZANIA. SOUTHERN HIGHLANDS: Poroto Mts., *Geilinger 2611* (K, Z); *McGregor 3* (K, EAH). Between Chunya and Mbeya, *Burtt 6225* (BM, BR, EAH, F, K). Chunya escarpment, *Richards 25795* (K). Njombe district, *Richards 6585* (K); *Gillett 17781* (EAH, K). Itaka, *Greenway 3651* (EAH, K, PRE). Mufindi, *Paget-Wilkes 261* (EAH, MO). Elton Plateau, *Richards 18460* (K, SRGH); *Davies s.n.* (K). SOUTHERN PROVINCE: 8 km W of Songea, *Milne-Redhead & Taylor 8377* (K). NORTHERN PROVINCE: Between Dongobesh and Mkulu, *Haarer 11613* (K). WESTERN PROVINCE: Sumbawanga, *Van Rensburg s.n.* (EAH).

ZAÏRE. SHABA (Katanga): Gare de Biano, *Schmitz 4893* (BR, WAG). Kipopo, *Schmitz 5495* (BR). Parc Nationale de l'Upemba, *Robyns 3940* (BR). 70 km S of Jadotville, *Schmitz 4055* (BR). Lubudi, Kendo, *de Witte 537* (BR, WAG, Z).

ZAMBIA. NORTHERN REGION: Mbala (Abercorn) district, Lumi River flats, *Richards 5844* (BR, K, SRGH). Ndundu, Mbala district, *Richards 13138* (K, SRGH). Mansa (Fort Rosebery), *Fries 608* (UPS). N of Lake Shiwa Ngandu, *Greenway & Trapnell 5709* (EAH). CENTRAL REGION: Serenje, *Fanshawe 6727* (SRGH). EASTERN REGION: Nyika Plateau, *Robinson 3012* (K, M, PRE, SRGH). WESTERN REGION: N of Kakema River, Mwinilunga district, *Milne-Redhead 965* (PRE).

10. **Moraea muddii** N. E. Brown, Trans. Roy. Soc. S. Africa 27: 346. 1929. TYPE: South Africa, Transvaal, Mac Mac Creek, Sabie district, *Mudd s.n.* (K, holotype).

Plants 15–40(–70) cm high, solitary. *Corm* ca. 1.5 cm in diameter; tunics fine, usually pale. *Prophylls*, short, dry, pale brown, usually irregularly broken. *Leaf* linear, canaliculate ca. 5 mm wide, exceeding the inflorescence. *Stem* un-

branched. *Bract leaves* 2–4, herbaceous, 8–12 cm long. *Spathes* herbaceous; inner spathe 7–12 cm long, the outer ca. ¾ the inner. *Flowers* yellow; *outer tepals* lanceolate, 3.5–5 cm long, the limb 2–3 cm long; *inner tepals* to 3.5 cm long, erect. *Filaments* to 1 cm long, free in the upper third; *anthers* 8–11 mm long. *Ovary* ca. 1.5 cm long; style branches to 1.3 cm long, the crests to 1 cm long. *Capsule* ca. 2 cm long; *seeds* flattened and disc shaped. Chromosome number not known.

Flowering time: Late August to November.

Distribution: Eastern mountains of southern Africa, from the eastern part of the Cape Province to the Chimanimani Mountains of Rhodesia and Mozambique; usually in wet situations in grassland.—Fig. 9.

The few collections of a rather short, large yellow-flowered *Moraea* from the Chimanimani Mountains of Rhodesia and Mozambique match very closely *M. muddii*, a species previously recorded only from South Africa. The Chimanimani plants resemble *M. muddi* not only in form, but like it, are early blooming, and generally occur in moist habitats.

The range of *M. muddii* extends from the Chimanimanis south, along the eastern escarpment of South Africa to the Hogsback in the eastern Cape. The Rhodesia-Mozambique plants differ mainly in their rather early flowering, from August to September, in contrast to October to November in South Africa, but otherwise correspond very closely.

Moraea muddii is related to the *M. spathulata* complex, particularly to solitary-growing species such as *M. moggii*, *M. hiemalis*, and *M. carnea*, amongst others, and is distinguished by its shorter size, often smaller flower, and early blooming habit.

Mozambique. manica & sofala: Near summit of Chimanimani Mts., *Grosvenor 195* (LISC, SRGH, UPS, WAG).

Rhodesia. eastern region: Chimanimani Mts., *Garley 177* (SRGH); *Loveridge A42* (SRGH). Bank of Bundi River, Melsetter district, *Whellan 2153* (SRGH).

11. **Moraea inyangani** Goldbl., sp. nov. type: Rhodesia, vlei on Mt. Inyangani, 8,000 ft, *Wild 5519* (SRGH, holotype; K, LISC, M, PRE, isotypes).—Fig. 7B.

Planta parva, 15–30 cm alta. *Tunicae* cormi pallidae, tenuissimae. *Folium* solitarium, canaliculatum, inflorescentium excedens. *Caulis* simplex ferens 3(–4) bracteis. *Spathae* herbaceae, interiora 5–8 cm longa, exterior paulo brevior. *Flores* luteis; *tepala exteriora* ca. 2.5 cm longa, limbo ca. 1.5 cm longo, effuso; *interiora* 1.5–2 cm, erecta. *Filamenta* 4 mm longa; *antherae* ca. 6 mm longae. *Germen* ca. 1.4 cm longum; rami styli 8–9 mm longi; cristae 4–8 mm longae.

Plants small 15–30 cm high. *Corm* to 1 cm in diameter; tunics of fine, pale fibers. *Prophylls* brown, papery, irregularly broken. *Leaf* solitary, canaliculate, appearing terete with the margins tightly inrolled, to 3 mm wide and exceeding the inflorescence. *Stem* unbranched. *Bract leaves* 3(–4), herbaceous, 5–8 cm long. *Spathes* herbaceous with dry, brown acute apices; inner spathe 5–8 cm long, the outer only slightly shorter. *Flowers* pale yellow; *outer tepals* ca. 2.5 cm long, lanceolate, the limb ca. 1.5 cm long, spreading; *inner tepals* erect, 1.5–2 cm long. *Filaments* 4 mm long, free in the upper half; *anthers* ca. 6 mm

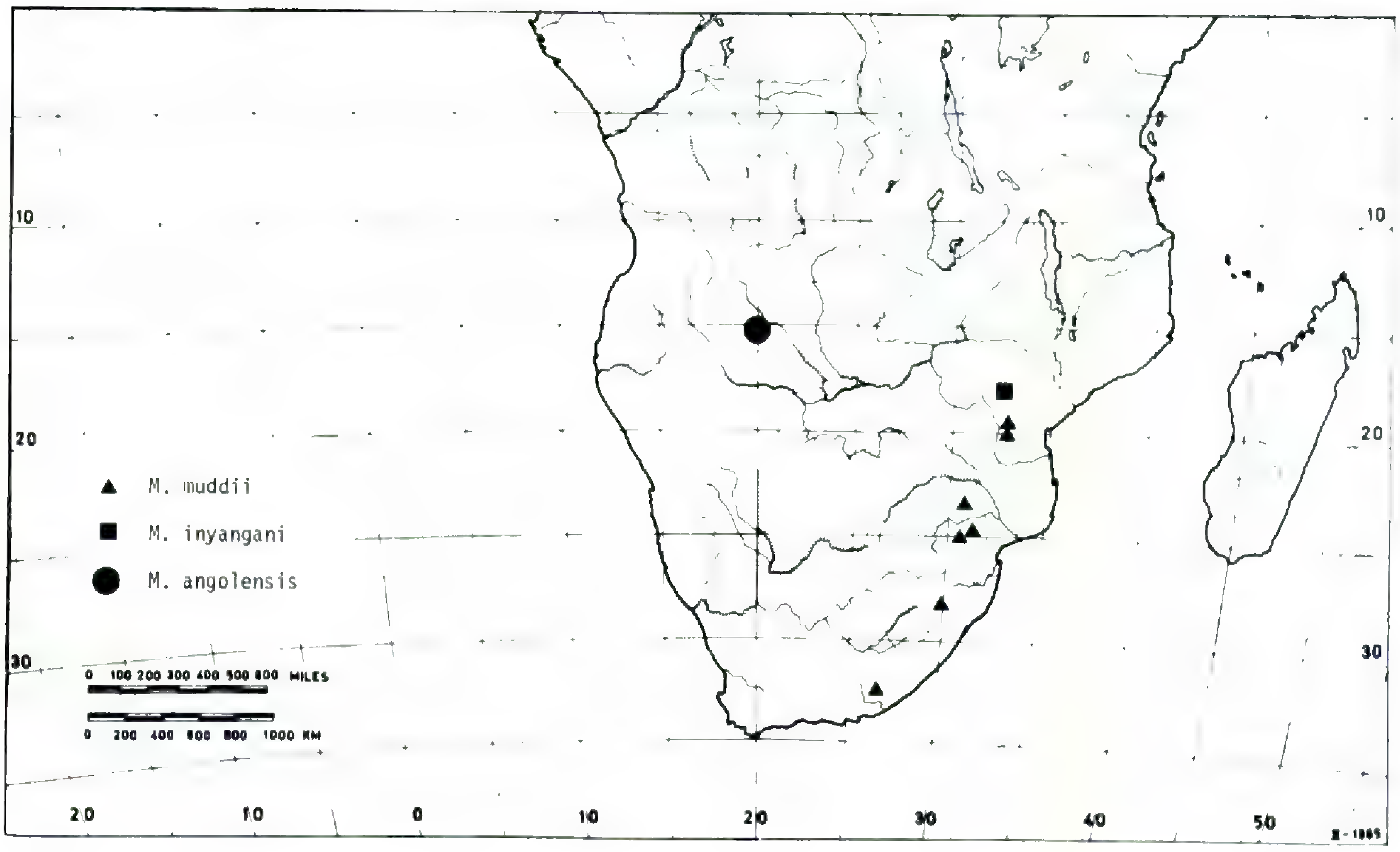

FIGURE 9. Distribution of *Moraea muddii*, *M. inyangani*, and *M. angolensis*.

long. *Ovary* ca. 1.4 cm long; style branches 8–9 mm long, the crests 4–8 mm long. *Capsule* and *seeds* unknown. Chromosome number not known.

Flowering time: September to October (also in April).

Distribution: Rhodesia, endemic on Mount Inyangani, Inyanga district, in moist situations at high altitudes.—FIG. 9.

The distive, small-flowered *Moraea inyangani* appears to be a very local species, having been recorded only from the higher altitudes of Mount Inyangani, in the Inyanga Highlands of Rhodesia. It is most closely related to *M. muddii*, which occurs to the south on the Chimanimani mountains of Rhodesia and Mozambique and in South Africa. *Moraea muddii* has a larger flower and a canaliculate leaf in contrast to the subterete leaf of *M. inyangani*. Both species appear to occupy the same habitat, high altitude grassland in moist situations, and both flower early in spring.

RHODESIA. EASTERN REGION: Inyanga district, Mt. Inyangani, *Leech 8140* (SRGH); *Corby 808* (K, SRGH). Summit ridge of Inyangani, damp flush, *Drummond & Robson 5830* (K, PRE, SRGH). Inyangani, wet flush below summit, *Boughey 264* (SRGH). Vlei on Mt. Inyangani, *Wild 5519* (K, LISC, M, PRE, SRGH); *Burrows 570* (SRGH).

12. **Moraea angolensis** Goldbl., sp. nov. TYPE: Angola, Moxico, Rio Culiti, *Capello & Ivens 18* (LISU, holotype).

Planta graciles. *Folium* solitarium. *Caulis* 35–40 cm alta, bracteis tria, illa 4–4.5 cm longa. *Spatha* 4–5 cm longa. *Flores* parvi; *tepala exteriora* ca. 3.5 cm longa, ungues ca. 2 cm; *tepala interiora* ca. 3 cm longa. *Filamenta* ad 11 mm longa, libera ad apicem 2 mm; *antherae* 6 mm longae. *Germen* 1–1.2 cm longum; rami styli ca. 8 mm longi; cristae ca. 8 mm longae.

Plants slender, 35–40 cm tall. *Corm* unknown. *Leaf* solitary, basal, ca. 2 mm wide and much exceeding the inflorescence, channeled. *Stem* erect. *Bract leaves*

3, 4–4.5 cm long with dry brown apices. *Spathes* 4–5 cm long, herbaceous, with the upper 5 mm dry and brown; outer spathe about ⅔ as long as the inner. *Flowers ?* yellow; *outer tepals* ca. 3.5 cm long, the claw 2 cm long; *inner tepals* ca. 3 cm long. *Filaments* to 11 mm long, free near the apex for 2 mm; *anthers* 6 mm long. *Ovary* 1–1.2 cm long; style branches ca. 8 mm long, the crests to 8 mm long. *Capsule* and *seeds* unknown. Chromosome number unknown.

Flowering time: August.

Distribution: Plains of southeastern Angola.—FIG. 9.

It is with some hesitation that I describe this species as it is based on two very poorly preserved specimens. The holotype and only gathering was collected by Capello and Ivens in August 1885 on their expedition across Africa from Angola to Mozambique. Dr. I. Melo of the University of Lisbon and Dr. E. Mendes, Director of the Junta de Investigacoes do Ultramar, Lisbon, Portugal have kindly aided me in localizing the place of collection, Rio Culiti, as southeastern Angola between latitude 14°50′S and 15°50′S and longitude 19°20′E and 21°50′ E. No other species of *Moraea* are known from anywhere near this area. The plants are quite different from any other tropical African species, perhaps most resembling *M. muddii* and *M. inyangani* both from the highlands of southeast Africa. The slender form, very short bracts and spathes, combined with a small flower make it easily distinguishable from these.

ANGOLA: MOXICO, Rio Culiti, *Capello & Ivens 18* (LISU).

13. **Moraea bella** Harms, Bot. Jahrb. Syst. 28: 364. 1901. TYPE: Tanzania, Southern Highlands, Uhehe, *Goetze 698* (B, holotype).—FIG. 10.

Plants solitary, slender, (30–)40–60(–70) cm high, very rarely branched. *Corm* ca. 1.5 cm in diameter; tunics of pale medium to coarse reticulate fibers. *Prophylls* small, light brown, dry and irregularly broken. *Leaf* solitary, canaliculate, 2.5–6 mm wide, inserted at ground level, and exceeding the inflorescence. *Stem* slender. *Bract leaves* 2–4, widely spaced, 6–7 cm long. *Spathes* dry and brown in the upper part or entirely so; inner spathe 6–10 cm long, the outer ½ to ⅓ the length of the inner. *Flowers* pale yellow, with a darker nectar guide and often conspicuously veined and spotted; outer tepals 4.5–5.5(–6.5) cm long, the limb 2.5–4 cm, spreading; *inner tepals* 3.5–5(–6) cm long, erect. *Filaments* 9–14 mm long, free in the upper third; *anthers* 8–10 mm long. *Ovary* 1.5–2 cm long; style branches 1.3–1.6 cm, the crests 0.8–1.5 cm long. *Capsule* ovate-oblong, 2–3 cm long; *seeds* flattened, ± triangular to discoid. Chromosome number not known.

Flowering time: (Late February) March to June (July).

Distribution: Northern Mozambique, Tanzania, Malawi, Zambia, Zaïre; only in seasonally or permanently waterlogged habitats such as marshes, vleis, dambos; flowering towards the end of the wet season and in the dry season.—FIG. 10.

Moraea bella can readily be recognized by the combination of several morphological features and its moist habitat and late flowering. It is a slender plant

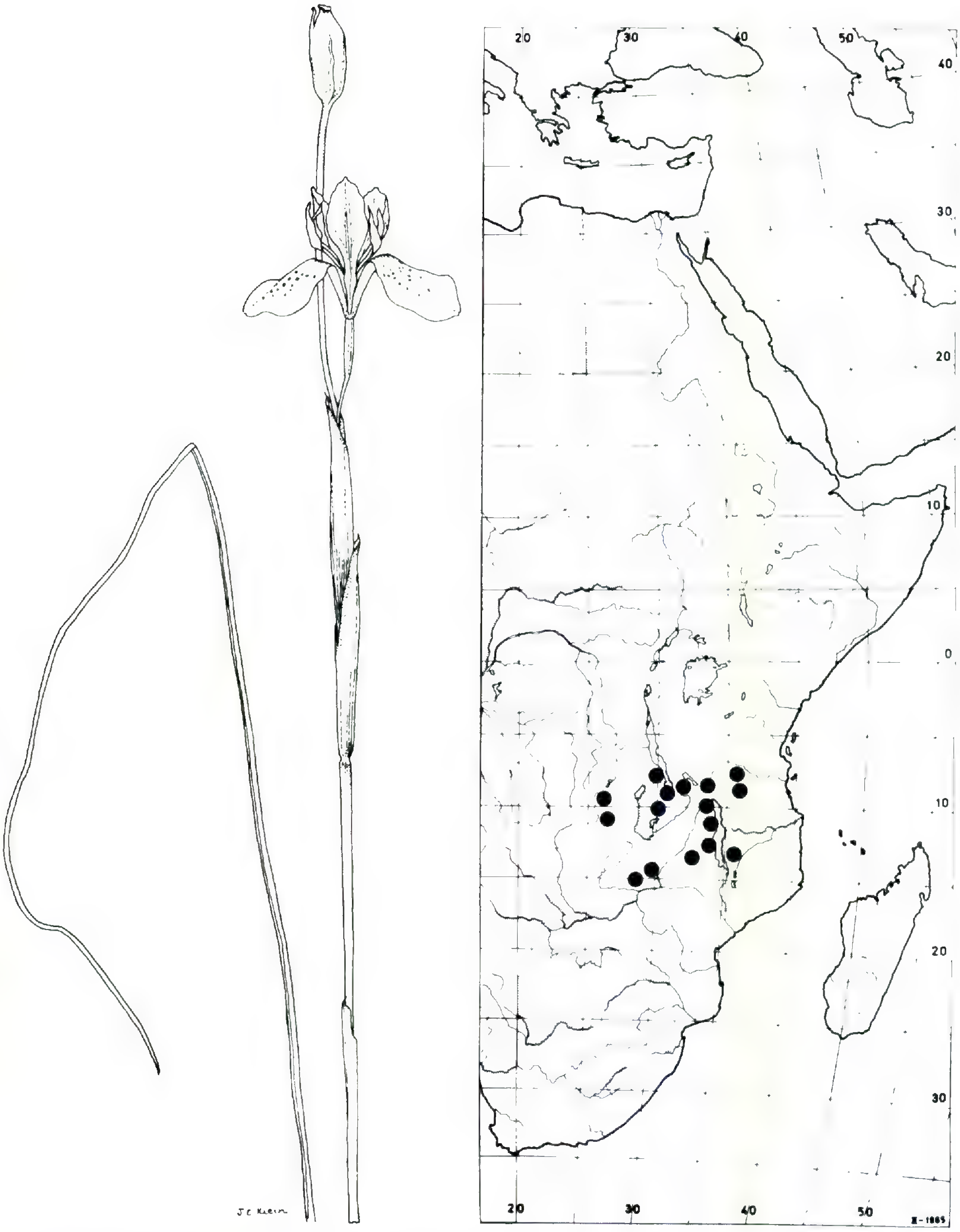

FIGURE 10. Morphology and distribution of *Moraea bella* (×0.5).

with a long, narrow leaf, and 2–4 comparatively short, widely spaced bract leaves. The yellow flowers, which are sometimes characteristically speckled, appear from late February through the end of the wet season and well into the dry season in July. The peak flowering period for the species is in April. *Moraea bella* is almost invariably found in very wet situations, usually in dambos but

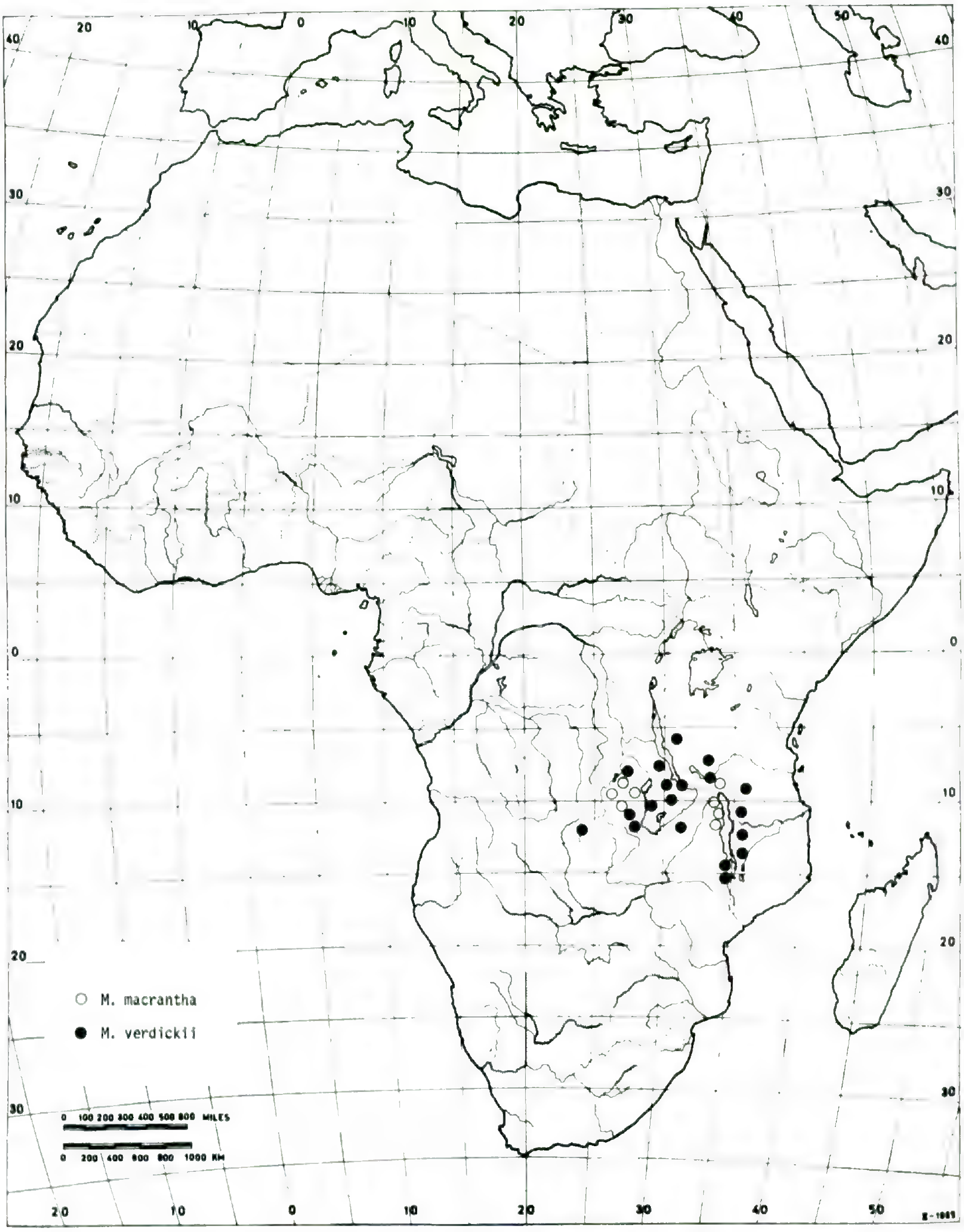

FIGURE 11. Distribution of *Moraea verdickii* and *M. macrantha*.

on occasion simply in damp, poorly drained grassland which retains moisture well after the rains are over.

Though described early this century, the name *M. bella* has been until now overlooked. Plants belonging to this species have either been assigned to *M. angusta*, a common and quite unrelated Cape species, or were included in other species, as for example by Geerinck (1970) who included specimens of *M. bella*

in his very broad concept of *M. textilis*. *Moraea bella* is closely related to *M. verdickii*, a larger-flowered species with the same general range and to the *M. macrantha-ventricosa-textilis* complex of south central Africa.

MALAWI. NORTHERN REGION: Mzimba, *Benson 1195* (K), *1339* (BM). Malembo, Mzimba district, *Pawek 8460* (K, MO, SRGH). Fort Hill, *Whyte s.n.* (K). Near Fort Hill, *Pole Evans & Erens 705* (BR, K, PRE, SRGH). Chelinda bridge, Rumphi district, *Pawek 2196* (K). CENTRAL REGION: Mchinji district, *Brummitt 10206* (K). Kasungu Game Reserve, *Brummitt 11603* (K); *Hill-Martin 1776* (PRE, SRGH). 22 km S of Kasungu, *Moriarty 355* (MAL).

MOZAMBIQUE. NIASSA: Vila Cabral, *Pedro & Pedrogao 3629* (EAH).

TANZANIA. SOUTHERN HIGHLANDS: Iringa, *Lynes 269* (K); *Pedersen 990* (DSM); *van Rensburg 677* (K). Between Iringa and Dabaga, *Eggeling 6122* (BR, EAH, K). Lunzua Agricultural Station, marsh, *Richards 5173* (BR). WESTERN PROVINCE: 65 km S of Sumbawanga, *Leach & Brunton 10072* (K, LISC, SRGH). Ufipa district, Isopa, *Robertson 641* (K, WAG).

ZAÏRE. SHABA: Near Kapona, Plateau des Muhila, *Schmitz 1652* (BR). Marungu-Katomia, *van den Bromde 1* (BR). Jadotville, vallée de la Mulende, *Dubois 1274* (K), *1074* (WAG). Kankela Valley, Manika Plateau, *Malaisse 8564* (BR).

ZAMBIA. EASTERN REGION: Chipata (Fort Jameson) *Fanshawe 4501* (EAH, K, SRGH); *van Rensburg 2111* (K, SRGH); *Munch 459* (K, LISC, SRGH). Lundazi, *Fanshawe 9291* (K, SRGH). Lukusuzi Game Reserve, *Sayer 205* (SRGH). CENTRAL REGION: Chakwenga headwaters, E of Lusaka, *Robinson 6473* (K, SRGH). Kawambura, *Fanshawe 3674* (K). Between Undaunda and Rufunsa, *Kornas 1519* (K). NORTHERN REGION: N of Mbala (Abercorn), *Greenway 6219* (K, EAH, PRE). "Fwambo," *Nutt s.n.* (K); *Carson s.n.* (K). Mbala district, Kawimbe road, *Richards 21407* (K, MO); *Sanane 1225* (K, PRE); *Robertson 618* (EAH, K); *Richards 897* (K), *1367* (K). Kambole escarpment, *Richards 9989* (K). Chisinga Ranch near Luwingu, *Astle 524* (K, SRGH), *3017* (SRGH).

14. **Moraea verdickii** De Wild., Ann. Mus. Congo, Sér. 4, Bot. 1: 17. 1902. TYPE: Zaïre, Shaba, Lukafu, *Verdick 281* (BR, holotype).—FIG. 12A.

Plants large, 45–75 cm high, unbranched. *Corm* ca. 2 cm in diameter; tunics coarse, of pale or occasionally dark fibers. *Prophylls* pale to dark brown, dry, broken and fibrous apically. *Leaf* linear, shortly exceeding the inflorescence, canaliculate or ± flat, 4–12 mm wide, inserted near the base but often up to 10 cm above ground. *Stem* bearing 2–3(–4) herbaceous bract leaves, usually widely spaced but occasionally overlapping. *Spathes* herbaceous, with a brown, acute apex; inner spathe 9–15 cm long, the outer ca. ⅔ the inner. *Flowers* yellow; *outer tepals* (5–)6–7.5(–10) cm long, the limb 3–5 cm long, spreading; *inner tepals* erect, 4.5–7 cm long. *Filaments* 11–16 mm long, free in the upper third; *anthers* (10–)11–14 mm long. *Ovary* usually exserted, 1.5–2(–2.5) cm long; style branches 1.7–2.5 cm long, the crests 1–1.7 cm long. *Capsule* and *seeds* not known. Chromosome number not known.

Flowering time: Late November to February (March).

Distribution: Grasslands and open bush, occasionally in damper situations, in eastern Angola, northern and western Zambia, Zaïre, Tanzania, Malawi, and central Mozambique.—FIG. 11.

Moraea verdickii is one of the taller species of *Moraea* and has particularly large flowers. It occurs in a belt across south tropical Africa from eastern Angola through southern Zaïre and Zambia to Malawi, southwestern Tanzania and Mozambique. Though recognized as early as 1902 by De Wildeman, it has in the past been included in *M. ventricosa* in herbaria, and most recently was in-

FIGURE 12. *Moraea* species.—A. *M. verdickii*.—B. *M. ventricosa*.—C. *M. textilis* (×0.5).

cluded with *M. ventricosa* in *M. textilis* by Geerinck (1970) who held a very broad concept of this species.

A detailed and critical comparison of a large number of specimens of *M. verdickii* and its close allies, *M. ventricosa*, *M. textilis*, and also including the related *M. macrantha* was made in the course of this study. In my estimation the best solution to the systematics of this group is to recognize all four species. *Moraea verdickii* can be distinguished from its close allies by its large, consistently yellow flower, with the outer tepals ranging from (5–)6–10 cm long and the anthers (10–)11–14 mm long; few bract leaves, generally 2 or 3; its habitat, grassland and open bush; and its early flowering, from late November to February, occasionally until March. *Moraea macrantha* has similar large flowers which are always dark blue, has 4–5 bract leaves, and flowers later, from mid February to July. *Moraea ventricosa* has smaller, blue or white flowers, 3–6 bract leaves, often grows in wet situations, and flowers from February to May; while *M. textilis*, with either yellow or blue flowers, generally has 5–7 bract leaves, and reaches peak flowering in May.

ANGOLA. MOXICO: Lusavo falls, *Milne-Redhead 4088* (BR, K).

MALAWI. CENTRAL PROVINCE: Dedza, *Jeke 79* (K, SRGH). Chongoni forest, Dedza, *Banda 526* (SRGH); *Salubeni 1253* (K, MAL, SRGH). Dedza mountain area, *Adlard & Chapman 561* (K, LISC, SRGH). Kirk Range, Ncheu-Neno road, *Robson 1404A* (K, LISC, SRGH).

MOZAMBIQUE. NIASSA: 80 km from Mijjao de Massangulo to Vila Cabral, *Correia 154* (LISC). Near Mtengula, *Seddon 7* (K). TETE: 8 km from Mlangeni, on Ncheu-Dedza road, *Brummitt 8609* (K, SRGH). Kirk Range, Ncheu-Neno road, *Robson 1404* (K). Massangulo, *Gomes & Sousa 1306* (K). ZAMBEZIA: Grirué near Vila Quanquiero, *Torre 5078* (LISC).

TANZANIA. SOUTHERN HIGHLANDS: Iringa district, 25 km S of Dabaga, *Polhill & Paulo 1560* (BR, EAH, K, LISC, PRE). 50 km N of Mbeya, *Bally & Carter 16475* (EAH, SRGH). Ca. 120 km N of Mbeya on Itigi road, *Boaler 843* (K). SOUTHERN PROVINCE: Matengo hills, Songea, *Milne-Redhead & Taylor 9024* (LISC, PRE, SRGH).

ZAÏRE. SHABA: SE Lubumbashi (Elisabethville), *Schmitz 3721* (BR). Near Lubumbashi, *Hirschberg 58* (PRE). Keyberg, *Schmitz 1230* (BR). Derubo, *Quarré 1008* (BR). Marie José, *Quarré 1524* (BR). Lupaku River, *Kassner 2466* (BR, K, Z). Marungu, Kisinde, *Dubois 1074* (BR, WAG). Mitwaba terr. River Kenia, *de Witte 2470* (K, SRGH).

ZAMBIA. NORTHERN PROVINCE: Kambole escarpment, *Richards 18881* (K, UPS). Itembwe Gorge, Mbala (Abercorn) district, *Richards 12055* (EAH, K, MO, SRGH). Itembwe Gap, *Richards 18830* (K, SRGH). Mbala, Kalambo falls road, *Richards 17080* (K, SRGH); *Bullock s.n.* (BR, K). Mpika, *Fanshawe 1890* (BR, K, SRGH). 40 km N of Mpika, *Williamson 1470* (K, SRGH). S of Nchelenga, Kawambwa district, *Williamson 1233* (SRGH). Chishinga ranch, *Astle 1395* (SRGH). WESTERN PROVINCE: Matonchi farm, Mwinilunga district, *Milne-Redhead 3930* (BR, K, LISC, PRE).

15. **Moraea macrantha** Baker, Fl. Trop. Africa 7: 340. 1898. TYPE: Malawi, Northern Province, without precise locality, *Whyte s.n.* (K, holotype).

M. arnoldiana De Wild., Ann. Mus. Congo, Sér. 4, Bot. 1: 16. 1902. TYPE: Zaïre, Shaba, Kasenga, Lukafu, *Verdick 606* (BR, holotype).

Plants solitary, unbranched, 50–70 cm high. *Corm* ca. 1.5 cm in diameter; tunics of pale fine to medium fibers. *Prophylls* brown, soft textured and irregularly broken to fibrous. *Leaf* solitary, linear, basal, canaliculate, to 7 mm wide, much exceeding the inflorescence. *Stem* unbranched. *Bract leaves* 4–5, herbaceous, usually overlapping, attenuate, 6–10 cm long. *Spathes* herbaceous, with a dry acute apex; inner spathe 9–13 cm long, the outer ca. ⅔ the inner.

Flowers blue violet with pale nectar guides; *outer tepals* (5.7–)6.5–8 cm long, the limb ± equal or exceeding the claw, 3.0–4.5 cm long; *inner tepals* 5.5–7.5 cm long, lanceolate. *Filaments* 1.3–1.7 cm long, free in the upper half to third; *anthers* 1.2–1.5 cm long. *Ovary* ca. 2 cm long, often enclosed in the spathes; style branches ca. 2.5 cm long, the crests to 2 cm. *Capsule* ca. 3 cm long; *seeds* flattened, ± triangular. Chromosome number $2n = 12$.

Flowering time: (Mid February) March to early July.

Distribution: Open woodland or montane grassland in northern Malawi, eastern Zambia, southwestern Tanzania, and Zaïre.—FIG. 11.

Moraea macrantha is closely related to *M. verdickii* and *M. textilis* (see discussion under *M. verdickii*). It can be distinguished from *M. verdickii* by its dark blue flowers, 3–5 bract leaves, and later flowering, from mid February to July; and from *M. textilis* by its generally larger flowers, with tepals in the 5.7–8 cm range, and anthers 1.2–1.5 cm long.

Moraea macrantha is apparently common in northern Malawi and relatively rare elsewhere, though it extends through southwestern Tanzania to the higher areas of Shaba in Zaïre. It occurs only in highland areas and flowers from mid- to late-wet season.

MALAWI. NORTHERN REGION: Vipya hills, *Chapman H 640* (SRGH). Vipya plateau, *Salubeni 660* (K, LISC, PRE, SRGH). Vipya link road, *Pawek 1060* (K, MAL, SRGH). Vipya, Luwawa, *Chapman 1632* (K, SRGH). Mzuzu, *Pawek 5396* (K, MO, SRGH), *5832* (MO, SRGH), *2448* (K, MAL). Mzimba district, *Jackson 1283* (BM, BR, K, MAL). Rumphi district, *Pawek 3595* (K, MAL). Nyika Plateau, *Pawek 6696* (MO, PRE). Chitipa, between Misuku hills and Kalenje River, *Pawek 5170* (K, MAL, MO, SRGH). 30 km S of Chikangawa, Vipya Mts., *Brummitt 10470* (K). Wenya, *Benson 1325* (BM). Mafinga Mts. near Chisengo, *Chapman 1864* (SRGH).

TANZANIA. SOUTHERN HIGHLANDS: Ulanda, Ulambya, *Leedal 599* (EAH). Kasebe, Bundali, *Leedal 439* (EAH).

ZAÏRE. SHABA: Lukafu, Mutoli-Tuli, *Verdick s.n.* (BR). Parc Nationale de l'Upemba, Pandeluru, *de Witte 2611* (BR). Plateau des Kundulungu, *Lisowski, Malaisse & Symoens 11621* (BR). Kibura Plateau, 25 km N of Mitwaba, *Lisowski, Malaisse & Symoens 13676* (BR). 5 km S of Poste de Katshupa, *Lisowski, Malaisse & Symoens 5798* (BR).

ZAMBIA. EASTERN PROVINCE. Nyika Plateau, *Richards 14388* (K).

16. **Moraea ventricosa** Baker, Bull. Misc. Inform. 1895: 13. 1895. TYPE: Zambia, Northern Province, "Fwambo," *Carson 37/1894* (K, holotype).—FIG. 12B.

M. bequaertii De Wild., Repert. Spec. Nov. Regni Veg. 11: 540. 1913. TYPES: Zaïre, Shaba (Katanga), Lubumbashi, *Bequaert 316* (B, lectotype). Zaïre, Tshisenda, *Ringoet 419* (BR, syntype); *Homblé 360* (BR, syntype). Zaïre, Lubumbashi, *Homblé 238* (BR, syntype).

Plants medium, 30–45 cm high, unbranched. *Corm* ca. 1.5 cm in diameter; tunics of pale medium to fine fibers. *Prophylls* pale to dark brown, broken and becoming fibrous. *Leaf* exceeding the inflorescence, linear, canaliculate, 3–7 mm wide. *Stem* bearing 3–5(–6) overlapping, herbaceous bracts. *Spathes* herbaceous; inner spathe 8–11.5(–13.5) cm long, the outer ca. ⅔ the inner. *Flowers* comparatively small, blue purple or white to pale yellow; *outer tepals* 4–5(–5.5) cm long, the limb equal or slightly shorter than the claw; *inner tepals* 3.7–4.5 cm long. *Filaments* 12–15 mm long, free in the upper third; *anthers* 8–10(–11) mm long. *Ovary* ca. 2 cm long; style branches 1.4–1.7 cm long, the crests ca. 1

cm long. *Capsule* ovoid, to 3 cm long; *seeds* not known. Chromosome number $2n = 12$.

Flowering time: Late February to early May (one record from September).

Distribution: Burundi, western and southern Tanzania, southeastern Zaïre, and northern and western Zambia; open woodland or grassland, often in moister places along the margins of dambos, marshes, etc.—FIG. 13.

Moraea ventricosa as treated here includes both white (to pale yellow) and blue, small-flowered plants. It is one of the few species of subgenus *Grandiflora* where forms with different colored flowers are known. White-flowered plants occur in the eastern part of its range in western Tanzania, Burundi, and north-eastern Zambia, while blue-flowered plants predominate to the west, in Zaïre and northwestern Zambia, *M. bequaertii* from Zaïre exemplifying the latter. Though recorded from open woodland or grassland, *M. ventricosa* is more often found in moist situations as along dambo margins or poorly drained areas.

As discussed under *M. verdickii*, *M. ventricosa* is part of a complex of closely allied species including *M. macrantha* and *M. textilis*. In fact, it appears most closely related to the Angolan *M. textilis* which generally has larger flowers, with outer tepals in the 5–6 cm range and anthers 10–13.5 mm long. Specimens of *M. verdickii* have in the past usually been included in *M. ventricosa*, but the larger yellow flowers of the former, as well as its earlier blooming habit, should be sufficient to prevent confusion.

BURUNDI. Gitega, Burasira, *Lewalle 1728* (BR, K, WAG). Vicinity of Karuzi-Bureru, *van der Ben 1966* (K).

TANZANIA. SOUTHERN HIGHLANDS: Mtengulu, Kyimbila district, *Stolz 2625* (BM, BR, K, PRE). Elton Plateau, S of Chimala, *Milton 72* (EAH). Tunduma, *Moreau & Moreau 9807* (EAH). Tunduma-Sumbawanga, *Leedal 1076* (EAH). WESTERN PROVINCE: Ufipa district, vlei near Zambia border, *Whellan 1212* (K, MAL, SRGH). Near Chapota, Sumbawanga, *Richards 8507* (K). Lake Kwela, *Bullock 2650* (K). Kundi, *Bullock s.n.* (K).

ZAÏRE. SHABA: Lubumbashi (Elisabethville), Boitsfort, *Robyns 1655* (BR, EAH, WAG). Lubumbashi, *Bequaert 316* (BR); *Hirschberg 58* (K). Vallée de Lubumbashi, *Quarré 3179* (BR, WAG). Kipopo, *Thoen 4646* (BR); *Schmitz 5835* (BR). Lopoto, *Schmitz 4855* (BR). Kafubu, *Quarré 182* (BR, WAG). Vallée de Kapiri, *Homblé 1238* (BR). Tshinsinka, Manika (Biano) Plateau, *Homblé 1275* (BR).

ZAMBIA. NORTHERN PROVINCE: Mbala (Abercorn) district, Lumi River Marsh, *Richards 12278* (SRGH). Kawimbe, *Richards 8329* (K), *19038* (K, MO). Kali, dambo, *Richards 4976* (K). WESTERN PROVINCE: Solwezi, *Drummond & Rutherford-Smith 7031* (BR, K, LISC, M, PRE, SRGH). Ndola, *Fanshawe 969* (BR, EAH, K, SRGH). Kitwe, *Fanshawe 10142* (SRGH); *Mutimushi 267* (SRGH), *2546* (K). Mutufa River, *Lawton 237* (K). Shibuchinga, *Fanshawe 8388* (K, SRGH). Mwinilunga district, *Marks 42* (K). Kabompo road, 25 km from Mwinilunga, *Edwards 676* (LISC, PRE, SRGH).

17. **Moraea textilis** Baker, Trans. Linn. Soc., London Bot., Ser. 2, 1: 270. 1878. TYPE: Angola, Huila, Lopollo River, flowering in April, *Welwitsch 1549* (BM, holotype; COI, K, LISU, isotypes).—FIG. 12C.

M. mechowii Pax, Bot. Jahrb. Syst. 15: 151. 1893. TYPE: Angola, Catala Canginga, flowering in Feb., *Teuscz in Exped. Mechow 557c* (B, holotype; BM, isotype).

Plants large, 40–80 cm high, unbranched. *Corm* ca. 2 cm in diameter; tunics of coarse, grey, wiry fibers. *Prophylls* rigid, pale, streaked with longitudinal dark veins and irregularly broken. *Leaf* linear, canaliculate, exceeding the in-

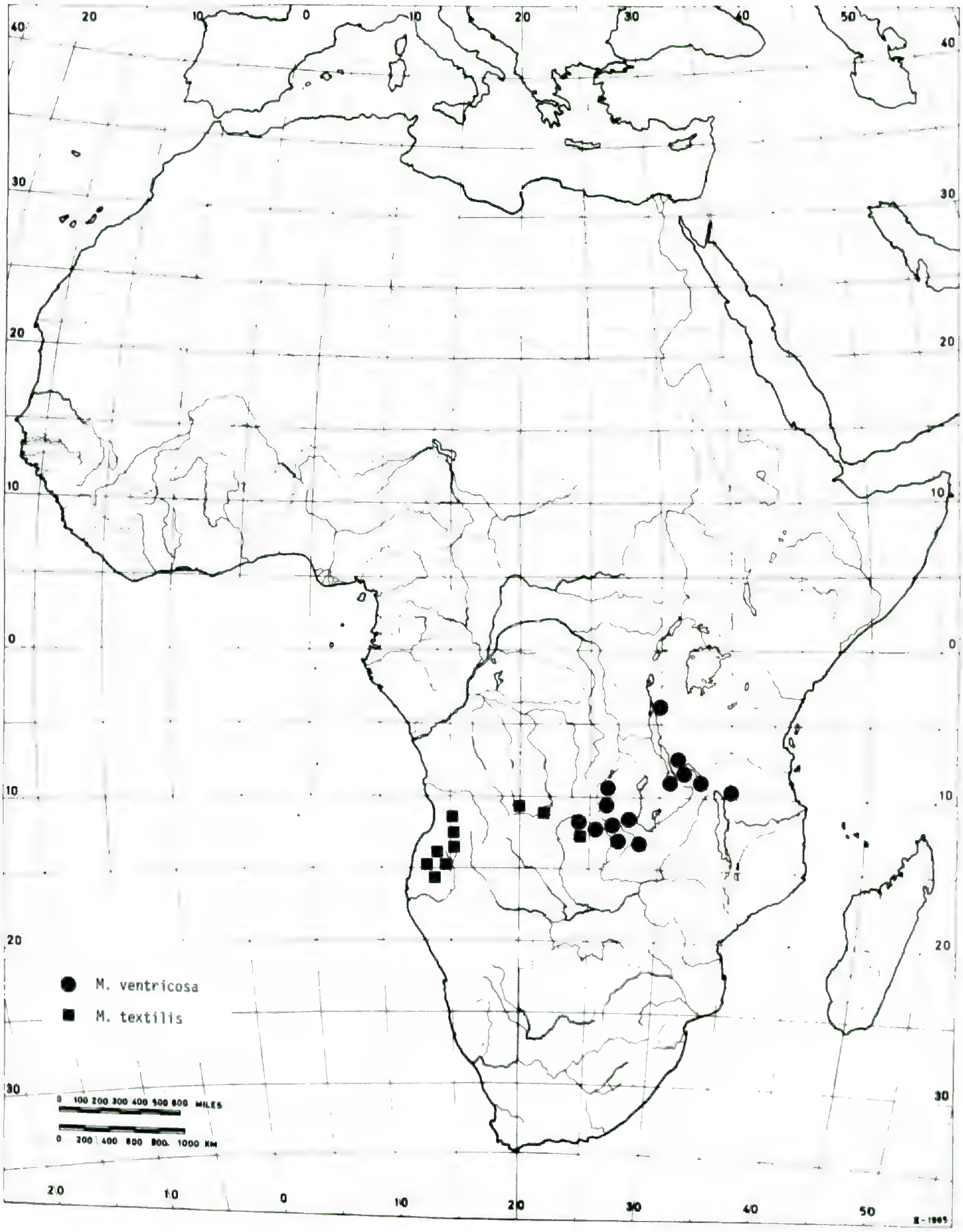

FIGURE 13. Distribution of *Moraea ventricosa* and *M. textilis*.

florescence, 6–8 mm wide. *Stem* bearing (3–)5–7, often dry and usually overlapping, bract leaves. *Spathes* herbaceous, becoming dry from above, acute, often becoming reddish; inner spathe 8–15 cm long, the outer ca. ¾ the inner. *Flowers* blue purple or yellow, usually conspicuously streaked with purple; *outer tepals* 4.7–6.3 cm long, the claw often slightly exceeding the limb; *inner tepals* erect, 4.8–6.5 cm long. *Filaments* 1.5–2.2 cm long, free in the upper quar-

ter; *anthers* 1.0–1.35 cm long. *Ovary* ca. 2 cm long; style branches 1.5–2.5 cm long, the crests to 1.5 cm long. *Capsule* ovoid, ca. 3 cm long; *seeds* flattened and triangular to discoid. Chromosome number not known.

Flowering time: (January) April to June (July to August).

Distribution: Throughout the Angolan plateau above 1,200 m in grassland or rocky sites, occasionally reported from damper situations.—FIG. 13.

A much more restricted concept of *M. textilis* is proposed here compared to Geerinck's (1970) treatment of this species which included *M. ventricosa* and *M. verdickii.* As treated here, *M. textilis* occurs almost exclusively in Angola, from the highlands in the southwest to the border of Zaïre and Zambia, one collection being known from western Zambia. Collections suggest that the species is common in the provinces of Huila and Huambo, and relatively rare elsewhere, though this may simply be a reflection of collecting activity being concentrated in population centers. *Moraea textilis* is reported from grassland and rocky sites at elevations above 1,200 m, though occasionally also from damp places. It has a remarkably long flowering period from December to July, though most collections are from the months of May and June, in the dry season.

Moraea textilis is most closely related to *M. ventricosa*, a somewhat smaller species occurring mainly in moist situations to the east, and it is also allied to *M. verdickii* and *M. macrantha* as discussed under *M. verdickii.* The latter invariably has yellow flowers which are larger than those of *M. textilis*, and it blooms in the wet season, from November to February and March.

ANGOLA. BENGUELLA: Highlands between Ganda and Caconda, *Hundt 822* (BM, Z). Bailono district, *Wellman 1906* (K). Caconda, *Gossweiler 4206* (COI). CUANZO SUL: Amboim, *Gossweiler 996K* (COI, K). HUAMBO: Huambo (Nova Lisboa), *da Silva 3604* (LISC). Between Huambo and Quipeio, *Exell & Mendonça 1874* (BM). Near Caululo, *Moreno 163* (COI, LISC). Cuima, *Exell & Mendonça 1937* (BM). Country of the Ganguellas and Ambuellas, *Gossweiler 4136* (K). Sacaala forest, *Murta 170* (COI). Mt. Moco, plateau above village, *Huntley 3430* (PRE). HUILA: Hoque, *Henriques 1020* (BM, COI, K, LISC, LISU, SRGH). Leba, *Pritchard 339* (BM, K, LISC). Near Lopollo River, *Welwitsch 1549* (BM, COI, K, LISU). Turdevala NW of Sa de Bandeira, *Kers 3294* (K, LISC, PRE, S); *Barbosa & Moreno 10218* (COI). Lubango, Buraco do Bimbe, *Mendes 3762* (LISC). Tchivinguiro, *Henriques 59* (LISC). LUNDA: R. Coxi, *Exell & Mendonça 1358* (BM). Xassengue Caiango, near River Cuando, *Gossweiler 11855* (COI). MOXICO: Texeira de Sousa, *Gossweiler 12248, 12249* (BM, LISC).

ZAMBIA. WESTERN PROVINCE: Plaius, Mwinilunga district, *Marks 42* (K).

18. **Moraea tanzanica** Goldbl., sp. nov. TYPE: Tanzania, Southern Highlands, Kyimbila district, *Stolz 2142* (K, holotype; BM, BR, GH, PRE, Z, isotypes). —FIG. 14A.

Planta 20–35 cm alta. *Tunicae* cormi pallidae. *Folium* solitarium, canaliculatum, 15–25 cm longum raro spathas excedentium, insertum breviter supra terram. *Caulis* simplex, ferens bracteis duabus. *Spathae* herbaceae, interior 9–10 cm longa, exterior 6–8 cm longa. *Flores* luteis; *tepala exteriora* 4.5–5.5 cm longa, limbis 3–3.5 cm longis, expansis; *interiora* 3.5–4.5 cm longa. *Filamenta* 1.2–1.5 cm longa; *antherae* ca. 1 cm longae. *Germen* 1.7–2.2 cm longum; rami styli 1.7–2 cm longi; cristae ca. 1.3 cm longae.

Plants solitary, medium, 20–35 cm high. *Corm* ca. 1.5 cm in diameter; tunics of pale medium fibers. *Prophylls* dry-membranous, pale, irregularly torn above. *Leaf* solitary, 15–25 cm long, seldom reaching beyond the midline of the spathes,

FIGURE 14. *Moraea* species.—A. *M. tanzanica.*—B. *M. clavata.*—C. *M. brevifolia.* (×0.5).

canaliculate, inserted shortly above ground level. *Stem* simple. *Bract leaves* 2, usually overlapping. *Spathes* herbaceous, attenuate; inner spathe 9–10 cm long, the outer ca. ⅔ the inner. *Flowers* yellow; *outer tepals* 4.5–5.5 cm long, the limb 3–3.5 cm long, spreading; *inner tepals* erect, 3.5–4.5 cm long. *Filaments* 1.2–1.5

cm long, free in the upper half; *anthers* ca. 1 cm long. *Ovary* 1.7–2.2 cm long; style branches 1.7–2 cm long, the crests ca. 1.3 cm long. *Capsule* cylindrical, to 3 cm long; *seeds* flattened, discoid. Chromosome number $2n = 12$.

Flowering time: January to March.

Distribution: Northern Malawi and southern Tanzania, at high altitudes, 2,000–3,000 m; in open mountain grassland.—FIG. 15.

Moraea tanzanica is related to the *M. textilis* complex, and particularly to the yellow-flowered *M. verdickii*. It is, however, a much smaller species, though with a very large flower, and can always be distinguished from *M. verdickii* by its consistently short leaf which seldom reaches beyond the midline of the spathes. *Moraea tanzanica* appears to stand at the beginning of a series of reduced species in which the leaf is generally short and inserted above ground level, sometimes at the base of the inflorescence. In this group the bract leaves are often congested and may be reduced in number or even lacking, as in *M. unifoliata*, the most specialized species in this alliance.

The species most closely related to *M. tanzanica* among the reduced species are *M. brevifolia*, which often has a shorter leaf and solitary bract leaf, and *M. clavata*, an early-flowering species with much smaller flowers. *Moraea tanzanica* is confined to southwestern Tanzania where it has been collected mostly at high altitudes in short grassland. It flowers from January to March, particularly towards the end of summer. In contrast, *M. brevifolia*, found to the west in Zambia, blooms in December to January and occurs only in marshy situations. *Moraea clavata*, flowering even earlier in late spring to mid summer, is also confined to moist situations and occurs from central Zambia to southern Angola.

MALAWI. NORTHERN REGION: Nyika Plateau, Katumbi-Juniper forest turnoff, *Pawek 6660* (MO); *Phillips 1071A* (K, MO, SRGH).

TANZANIA. SOUTHERN HIGHLANDS: Kyimbila district, *Stolz 2142* (BM, BR, GH, K, PRE, Z). Elton Plateau, *Richards 14128* (EAH, K). Rungwe Mt., *Richards 14314* (K). Rungwe caldera, *Pocs 6505* (DAR). Mbeya Peak, *Kerfoot 1628* (EAH). Kipengere Mts., Njombe district, *Richards 7574, 7617* (K). Ndumbi Forest Reserve, *Semsei 1664* (EAH, K).

19. **Moraea brevifolia** Goldbl., sp. nov. TYPE: Zambia, Northern Region, Lumangwe Falls, Mporokoso district, *Simon & Williamson 1483* (K, holotype; LISC, SRGH, isotypes).—FIG. 14C.

Plantae 25–50 cm alta. *Tunicae* cormi pallidae, tenues. *Folium* solitarium, breve, 5–20 cm longum, insertum in pars inferior caulis. *Caulis* simplex, ferens bractea una, raro dua. *Spathae* herbaceae, interior 7.5–12 cm longa, exterior 6–9 cm longa. *Flores* luteus; *tepala exteriora* 5–7 cm longa, limbis 3–4 cm longis, expansis; *interiora* 4–5 cm longa. *Filamenta* 10–12 mm longa; *antherae* 9–16 mm longae. *Germen* 1–1.3 cm longum; rami styli 1.2–2.5 cm longi; cristae ad 1.5 cm longas.

Plants 25–50 cm high, solitary. *Corm* 1–1.5 cm in diameter; tunics of fine brown reticulate fibers. *Prophylls* dry-membranous, becoming lacerated above. *Leaf* solitary, short, 5–20 cm long, with a free apex or entirely sheathing and bractlike, inserted in the lower half of the stem, above ground level, canaliculate. *Stem* simple. *Bract leaf* 1 (occasionally 2), 6–9 cm long. *Spathes* herbaceous, with brown attenuate apices; inner spathe 7.5–12 cm long, the outer ca. ½–⅔ the inner. *Flowers* yellow; *outer tepals* 5–7 cm long, the limb 3–4 cm long, spread-

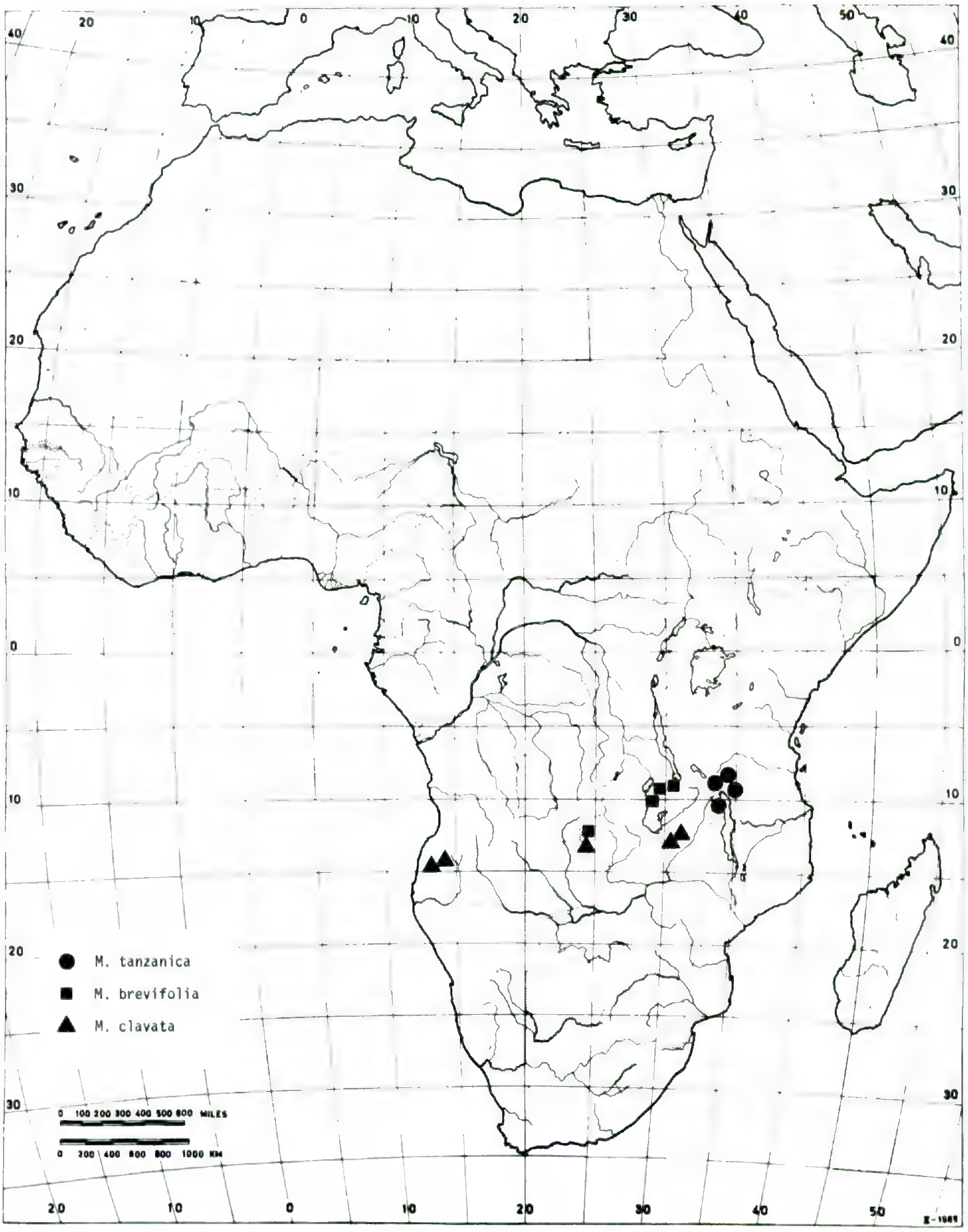

Figure 15. Distribution of *Moraea tanzanica*, *M. brevifolia*, and *M. clavata*.

ing; *inner tepals* erect, 4–5 cm long. *Filaments* 10–12 mm long, free in the upper third; *anthers* 9–16 mm long. *Ovary* 1–1.3 cm long; style branches 1.2–2.5 cm long, the crests to 1.5 cm long. *Capsule* and *seeds* unknown. Chromosome number not known.

Flowering time: December to January.

Distribution: Zambia, central to northeastern Zambia; in wet places.—Fig. 15.

Moraea brevifolia is apparently rare and occurs only in marshy situations in northern and western Zambia where it blooms in midsummer. It is somewhat variable in leaf morphology, some plants having a very short, almost entirely sheathing leaf, while in others the leaf is longer with the free portion reaching the spathes. The leaf is, however, distinctive in its point of insertion, well above ground, at about the midline of the stem. *Moraea brevifolia* is closely related to the predominantly Angolan *M. clavata*, a generally smaller species, which consistently has smaller flowers. *Moraea brevifolia* may also be confused with *M. tanzanica*, which has similar flowers, but is vegetatively more robust, has a larger broader leaf, and always has two bract leaves where one is the rule in *M. brevifolia.* These two species also differ in habitat and time of flowering, *M. tanzanica* being found in montane grassland and flowering later in the summer than *M. brevifolia.*

ZAMBIA. NORTHERN PROVINCE: Lumangwe Falls, Mporokoso district, *Simon & Williamson 1483* (K, LISC, SRGH). N'chelengi-Luapula River road, Kawambwa district, *Richards 15476* (K). Kambole-Mbala road, *Richards 11901* (K). Chinakila-Loye flats, Mbala district, *Richards 19473* (K). WESTERN REGION: Mwinilunga district, *Milne-Redhead 3930* (BM, BR, LISC). Plauis, Mwinilunga district, *Marks 41* (K).

20. **Moraea clavata** Foster, Contr. Gray Herb. 114: 49. 1936. TYPE: as for *M. gracilis* Baker.—FIG. 14B.

M. gracilis Baker, Trans. Linn. Soc. London, Bot., Ser. 2, 1: 271. 1878, hom. illeg. non *M. gracilis* (Licht. ex Roem. & Schult.) Diels, 1833. TYPE: Angola, Huila, near Lopollo River, *Welwitsch 1545* (BM, lectotype; K, LISU, isolectotypes).

Plants small, often growing in clumps, 15–30(–35) cm high. *Corm* 1–1.5 cm in diameter; tunics of fine, grey brown reticulate fibers. *Prophylls* short, membranous to herbaceous, usually entire at the apices. *Leaf* solitary, inserted midway up the stem, usually 5–12(–20) cm long, rarely exceeding the inflorescence. *Stem* simple with an extended lower internode. *Bract leaf* 1, herbaceous, 3–4 cm long, above the leaf. *Spathes* herbaceous with dry upper margins; inner spathe 4.5–6(–7) cm long, the outer ca. ⅔ the inner. *Flowers* yellow; *outer tepals* 2–3(–3.5) cm long, the limb 1–2 cm long, spreading; *inner tepals* 1.3–2.0 cm long, (probably) erect. *Filaments* 5–6 mm long, united in the lower half; *anthers* 4–5 mm long. *Ovary* 5–8 mm long; style branches ca. 1 cm long, the crests to 1.0 cm long. *Capsule* ovoid-globose, 7–10 mm long; *seeds* small, angular to somewhat flattened. Chromosome number not known.

Flowering time: October to January (March).

Distribution: Angola and Zambia, in moist situations.—FIG. 15.

Moraea clavata was among the first species of *Moraea* known from tropical Africa, having been collected in the 1850s by Welwitsch during his exploration of Angola. It was first named *M. gracilis* by Baker (in 1878) but this, a homonym, was replaced with *M. clavata* by Foster in 1936. Only a few collections are known, mainly from the southwestern highlands of Angola, but there are also records from western and northern Zambia, in the Mwinilunga and Serenje districts, the former some 800 km and the latter 1,500 km to the east of the Angola populations. It is a moisture loving species, found only in marshy places, dambos,

etc. and has a very long flowering period, from late spring in October to January, with one record in March.

It is a distinctive species, one of the smallest in subgenus *Grandiflora*, with a rather short leaf inserted well above ground level, a single bract, and a very small flower with an ovary 6–8 mm long. It is clearly related to *M. brevifolia*, a taller and larger-flowered species which grows in a similar habitat in western and northern Zambia. The difference in size between these two alone makes confusion unlikely.

ANGOLA. HUILA: Serra de Chela, Humpata, *Gossweiler 13315* (LISC). Humpata Plateau near Nhime, *Santos 76* (LISC). Huila, *Antunes s.n.* (LISU). Near the Lopollo River, *Welwitsch 1545* (BM, COI, K, LISU). Without precise locality, *Antunes 643* (LISC).

ZAMBIA. CENTRAL REGION: Serenje, *Fanshawe 6731* (K, SRGH). Road between Mpika and Kapiri-Mposhi, Serenje district, *Richards 16869* (K). WESTERN REGION: Mwinilunga district, dambo NE of Dobega Bridge, *Milne-Redhead 3620* (K).

21. **Moraea upembana** Goldbl., sp. nov. TYPE: Zaïre, Shaba, Parc Nationale de l'Upemba, banks of Lumana River, *de Witte 2400* (BR, holotype).—Fig. 16.

Planta parva, 10–20 cm alta. *Tunicae* cormi tenues, reticulatae. *Folium* ignotum, absens tempore florenti. *Caulis* simplex ferens 1–2 bracteis. *Spathae* herbaceae, interior 3.5–7 cm longa, exterior 3–4 cm longa. *Flores* luteis; *tepala exteriora* 2.7–4.5 cm longa, limbis 1.5–2.5 cm longis, expansis; *interiora* 2–2.5 cm longa. *Filamenta* ad 7 mm longa; *antherae* ad 8 mm longas. *Germen* 8–15 mm longum; rami styli ca. 10 mm longi; cristae ad 7 mm longas.

Plants small, 10–20 cm high, unbranched. *Corm* ca. 1 cm in diameter; tunics of pale to dark, finely reticulate fibers extending upward in a neck. *Prophylls* dry-membranous, entire or irregularly broken. *Leaf* unknown, absent at flowering time. *Stem* bearing 1 or 2 herbaceous bract leaves. *Spathes* herbaceous, with dry, pale brown acute apices; inner spathe 3.5–7 cm long, the outer 3–4 cm long, ca. half the length of the inner. *Flowers* yellow; *outer tepals* 2.7–4.5 cm long, the limb 1.5–2.5 cm long, spreading; *inner tepals* probably erect, 2–2.5 cm long. *Filaments* to 7 mm long; *anthers* to 8 mm long. *Ovary* 8–15 mm long; style branches ca. 10 mm long, the crests to 7 mm long. *Capsule* and *seeds* unknown. Chromosome numbers not known.

Flowering time: July.

Distribution: Zaïre, Shaba, apparently very local.—Fig. 17.

Known only from the type collection, this rare plant was placed by Geerinck (1970) in his treatment of *Moraea* in Zaïre and Burundi in *M. textilis*, according to his very wide interpretation of this species. It has however a number of very unusual features which make it appear to me quite distinct and perhaps not even very closely allied to *M. textilis*. Firstly, *M. upembana* flowers in July, in the dry season, is relatively short, standing up to 20 cm high, and is apparently quite leafless at this time. In contrast, *M. ventricosa* and *M. macrantha* (also included by Geerinck in *M. textilis*) normally flower in March and April in Shaba at the end of the wet season, and even those plants collected as late as May and June are as tall and as large flowered as the collections from earlier in the season, and do have a well-developed, green leaf. In other morphological features *M. upembana* also seems distinct, for it has very fine corm tunics, only 1 or 2 short

FIGURE 16. Type collection of *Moraea upembana*.

bract leaves, and is much smaller in all characteristics than *M. ventricosa* or *M. macrantha*, both of which have coarser corm tunics and 3–5 large bract leaves.

Though the single collection known is inadequate for a complete understanding of *M. upembana*, it seems best associated with the group of morphologically

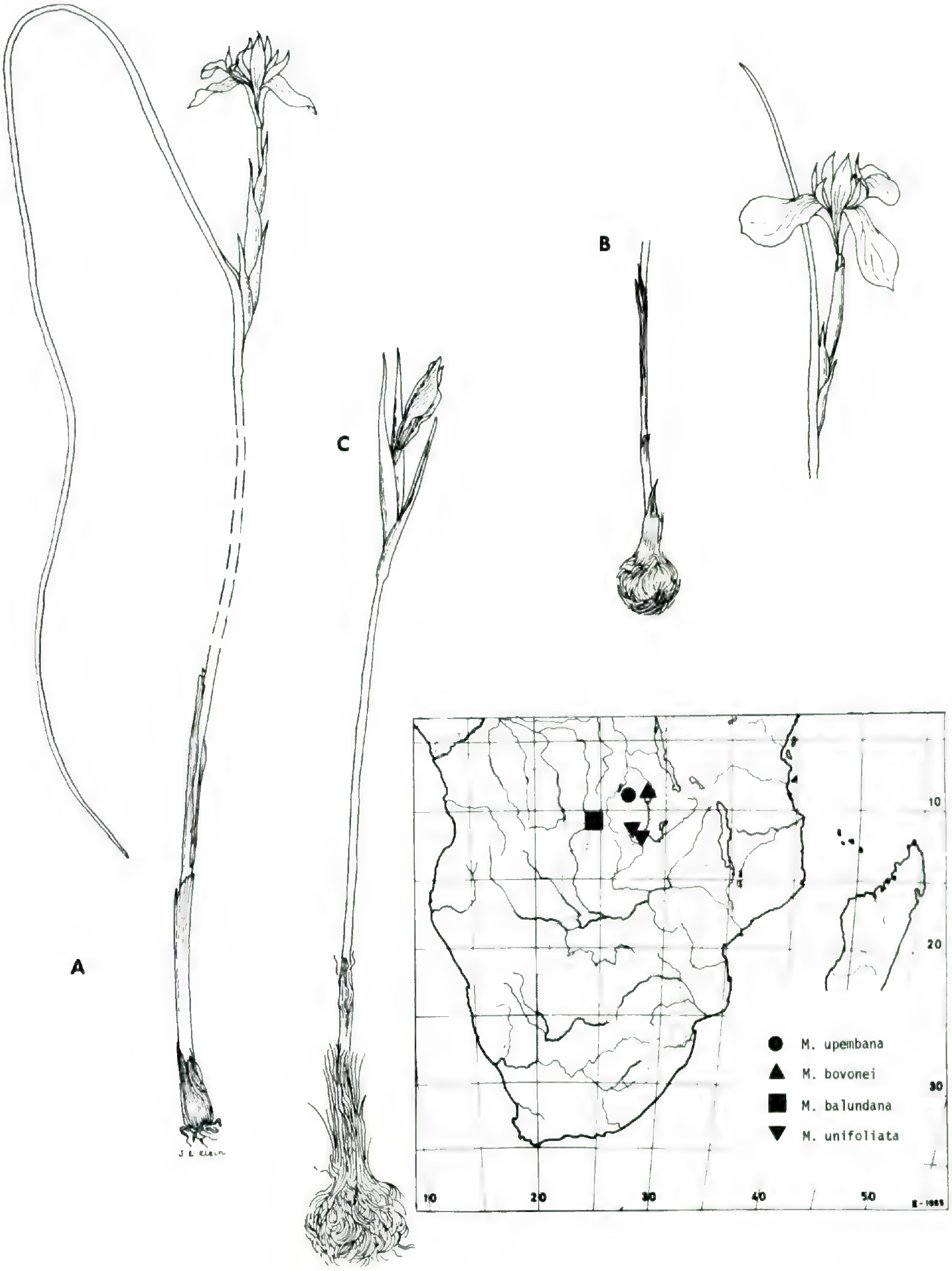

FIGURE 17. Distribution of *Moraea upembana*, *M. bovonei*, *M. balundana*, and *M. unifoliata* with morphology of—A. *M. bovonei*.—B. *M. balundana*.—C. *M. unifoliata* (×0.5).

reduced species of subgenus *Grandiflora*, and seems most closely related to the Angolan *M. clavata* and its relative *M. brevifolia* from Zambia. Further collections are needed to resolve the remaining questions about this species, including its habitat, variation pattern, and even the details of its leaf and flower structure.

ZAÏRE. SHABA: Parc Nationale de l'Upemba, Lumana River, *de Witte 2400* (BR).

22. **Moraea bovonei** Chiov., Nuovo Giorn. Bot. Ital. 26: 72. 1919. TYPE: Zaïre, Shaba, Ditungula, Lake Mweru, *Bovone 12* [F, lectotype; T (photograph seen) isolectotype].—FIG. 17A.

Plants slender, to 40 cm tall, with the leaf extending a further 40 cm. *Corm* and tunics not known. *Prophylls* papery, pale, becoming torn and irregular at the apices. *Leaf* terete, ca. 40 cm long, inserted at the base of the inflorescence. *Stem* with a long lower internode at the apex of which are 2 herbaceous bract leaves, each ca. 3.5 cm long, and the inflorescence. *Spathes* herbaceous with dry attenuate apices; inner spathe ca. 6 cm long, the outer slightly shorter. *Flower* yellow; *outer tepals* to 2.6 cm long; *inner tepals* to 2.4 cm long. *Filaments* ca. 8 mm long, united in the lower half; *anthers* 7 mm long. *Ovary* 8–10 mm long; style branches 1.2 cm long, the crests to 7 mm long. *Capsule* and *seeds* unknown. Chromosome number unknown.

Flowering time: Summer (February).

Distribution: Zaïre, eastern Shaba, marshes of Lake Mweru.—FIG. 17.

Moraea bovonei, known from only a single gathering, is a most unusual species. It has a very long slender stem, some 40 cm high, and the long leaf is inserted at the stem apex, immediately under the inflorescence. Unlike the related species, *M. balundana* and *M. unifoliata*, in which the leaf is also inserted below the inflorescence, the leaf of *M. bovonei* is very long, approximately equal in length to the stem. *Moraea bovonei* can be distinguished from its allies not only by its long stem and leaf but also by the presence of two bract leaves at the base of the spathes, whereas there is only one in *M. balundana* and none in *M. unifoliata.*

ZAÏRE. SHABA: Ditungula, Lake Mweru, *Bovone 12* (F, T).

23. **Moraea balundana** Goldbl., sp. nov. TYPE: Zaïre, Shaba, 52 km SW of Mutshatsha, *Robinson 6025* (K, holotype; M, SRGH, isotypes).—FIG. 17B.

Planta 15–40 cm alta. *Tunicae* cormi fuscae, tenues, reticulatae. *Folium* solitarium, insertum ad base inflorescentiae, 6–11 cm longum, teres. *Caulis* simplex, ferens bracteam unum. *Spatha* interior herbacea, 3–4.5 cm longa, exterior sicca, brunnea, 1.5–2 cm longa. *Flores* luteis; *tepala exteriora* 3–5 cm longa, limbis 1.7–3 cm longis, expansis; *tepala interiora* 2–3 cm longa. *Filamenta* 8–10 mm longa; *antherae* 8–9 mm longae. *Germen* ca. 8 mm longum; rami styli 1.2–1.5 cm longi; *cristae* 5–10 mm longae.

Plants slender and unbranched, 15–40 cm high. *Corm* ca. 1.5 cm in diameter; tunics of dark, finely reticulate fibers extending shortly upward in a neck. *Prophylls* membranous, but the upper one dry and becoming fibrous. *Leaf* 6–11 cm long, terete, inserted at the base of the inflorescence, and shortly exceeding it. *Stem* slender with a very long lowermost internode. *Bract leaf* 1, short, brown. *Spathes* unequal; inner spathe 3–4.5 cm long, herbaceous below, dry-brown at the apex, the outer 1.5–2 cm long, entirely brown, less than half the inner. *Flower* yellow; *outer tepals* 3–5 cm long, the limb 1.7–3 cm long, spreading; *inner tepals* 2–3 cm long, evidently erect. *Filaments* 8–10 mm long, free in the upper half; *anthers* 8–9 mm long. *Ovary* ca. 8 mm long; style branches

1.2–1.5 cm long, the crests 5–10 mm long. *Capsule* and *seeds* unknown. Chromosome number not known.

Flowering time: December.

Distribution: Zaïre, southwestern Shaba (Katanga) in permanently wet dambo.—Fig. 17.

Moraea balundana, known only from a single gathering in the southern part of Zaïre, close to the Angola and Zambia borders, is named after the Balunda tribe who live in this area. The species is closely related to *M. bovonei* which occurs to the east near Lake Mweru. *Moraea balundana* differs from *M. bovonei* mainly in its shorter leaf, single, dry, dark brown bract leaf, and unusually short, brown outer spathe. Further collections are needed to assess the variation in the species, and thus to better understand its relationship to the very similar *M. bovonei* and to *M. unifoliata*, also closely related. However, in the absence of more material, the unusual features of leaf, bracts, and spathes necessitate specific recognition. The species was assigned to *M. angusta* (Thunb.) Ker by Geerinck (1972), but the resemblance to this South African plant from the Cape region is only superficial. There seems no doubt that there is no close relationship between the two, assigned by Goldblatt (1976a, 1976b) to different subgenera of *Moraea*.

Zaïre. shaba, 52 km SW of Mutshatsha, near Zambian border, *Robinson 6025* (K, M, SRGH).

24. **Moraea unifoliata** Foster, Contr. Gray Herb. 114: 48. 1936. type: as for *M. aphylla* De Wild.—Fig. 17C.

M. aphylla De Wild., Ann. Mus. Congo, Sér. 4, Bot. 2: 21. 1913, hom. illeg. non *M. aphylla* L.f., 1781. type: Zaïre, Shaba (Katanga), Tembwe, *Hock s.n.* (BR, holotype).

Plants 20–35 cm high, unbranched. *Corm* ca. 1.5 cm wide; tunics of pale medium-fine reticulate fibers extending up in a neck. *Prophylls* papery, light brown, often fibrous above. *Produced leaf* of flowering individuals 4–6.5 cm long, seldom longer than the spathes, inserted near the apex of the stem and usually partly sheathing the inflorescence. *Stem* simple and lacking bract leaves. *Spathes* 4–6 cm long, herbaceous, or becoming dry, attenuate; inner spathe equal to or shortly exceeding the outer. *Flowers* yellow; *outer tepals* lanceolate, ca. 3.5 cm long, the claw to 1.5 cm long, spreading; *inner tepals* 2.5–3 cm long, erect. *Filaments* ca. 7.5 mm long, free in the upper part (half to a quarter); *anthers* 7.5–9 mm long. *Ovary* 7–10 mm long; style branches to 1.5 cm long, the crests 5–9 mm long. *Capsule* ovoid-globose, to 1 cm long, *seeds* not known. Chromosome number not known.

Flowering time: Late November to January.

Distribution: Zaïre, southern Shaba in moist situations along dambo margins or sponges.—Fig. 17.

Moraea unifoliata can immediately be recognized by its apparent lack of a produced leaf. It does, however, have a leaf which is inserted at the base of the inflorescence, but it is very short, and seldom extends more than 6 cm, thus not exceeding the inflorescence spathes. It is also distinctive in lacking bract leaves,

a feature which separates it from its close allies, *M. bovonei* and *M. balundana* in both of which the leaf is also inserted at the base of the spathes. The slender *M. bovonei*, however, has a very long leaf and two small bracts, while *M. balundana* has a shorter leaf and a single short, brown bract. These three species all grow in similar situations, moist sponges or along the margins of marshes or dambos, and bloom in summer. *Moraea unifoliata* is a fairly local species recorded from several sites, all in southern Shaba near Lumumbashi.

The singular habit of *M. unifoliata*, with its very short produced leaf placed immediately below the inflorescence and its complete lack of bracts, make the species appear one of the most specialized species of subgenus *Grandiflora*. It appears as the end product of a series of reduced species which begins with *M. tanzania* and *M. brevifolia*, and leads with progressive reduction in leaf size and bract leaf number through *M. clavata*, *M. balundana* and *M. bovonei*.

ZAÏRE. SHABA (Katanga): Mukuen, *Detilleux 175* (BR, WAG). Mukuen Est., *Schmitz 4250* (BR). Matuitui River, 10 km SSE of Lubumbashi (Elisabethville), *Schmitz 2371* (BR). Kapeluka, 16 km NE of Lubumbashi, *Schmitz 4766* (BR, WAG). Kipopo, 25 km NE of Lubumbashi, *Schmitz 8118* (BR, WAG). Marie-José, *Quarré 1478* (BR, GH).

INCOMPLETELY UNDERSTOOD SPECIES

The following taxon, represented by two collections, is problematic and may represent an undescribed species or a variant of a known one. Material is inadequate at present to provide a satisfactory solution.

Moraea *sp. 1*

Two collections only, of a very tall, large yellow-flowered species were made in the region of Lake Tanganyika. One, *Robyns 2192* was collected in Zaïre, between Pweto and Baudoinville, the other, *Wallace 1302*, was found in Tanzania. The plants are about 1 m tall and have large flowers which suggests that they may be forms of *M. verdickii*. They are, however, late flowering, in May, and have between 4 and 7 large bracts which in the Wallace collection are closely imbricate. Typically, *M. verdickii* blooms from December to February and rarely has more than three bracts, which do not overlap. The Robyns collection resembles to some extent *M. bella*, though it is unusually robust for this species and does not seem to fit in *M. bella* as presently circumscribed. Further material from this area is needed before a decision can be reached concerning these specimens.

EXCLUDED SPECIES

1. **Moraea revoluta** Wright

This species is excluded as the type material is teratological. The specimen, said to have been grown at Kew from corms collected in Angola, clearly belongs to subgenus *Grandiflora*, and the flowers resemble the pale form of *M. textilis*. Unique for the subgenus, however, are the several, linear, produced leaves. No other species or specimen of subgenus *Grandiflora* has more than a single leaf and the presence of more is almost certainly abnormal.

2. Several species of *Moraea*, described from Angola and Rhodesia, are now recognized as belonging to the genus *Ferraria*. Some have been transferred to *Ferraria* while others remain in *Moraea*. In spite of the multiplicity of names, there is probably only one species of *Ferraria* in the whole area including Angola, Zambia, Zaïre, and Rhodesia. The most commonly accepted name for the species is *F. glutinosa* (Baker) Rendle and the many synonyms originally placed in *Moraea* are listed below. *Ferraria glutinosa* is distinguished from *Moraea* by several features, the most readily observable being the equitant leaf, while the branched axis with sticky exudate below the internode are features lacking in the tropical African species of *Moraea*. It is further distinguished from *Moraea* by its long-lived, tuberlike corms which apparently lack tunics.

Ferraria glutinosa (Baker) Rendle, Cat. Afr. Pl. Welw. 2: 27. 1899.

Moraea glutinosa Baker, Trans. Linn. Soc. London, Bot., Ser. 2, 1: 271. 1878. TYPE: Angola, Huila, near Lopollo River, *Welwitsch 1543* (BM, holotype; LISU, isotype).
M. candelabrum Baker, Trans. Linn. Soc. London, Bot., Ser. 2, 1: 271. 1878. TYPE: Angola, Huila, Morro de Lopollo, *Welwitsch 1544* (BM, holotype; LISU, isotype).
M. andongensis Baker, Trans. Linn. Soc. London, Bot., Ser. 2, 1: 271. 1878. TYPE: Angola, Pungo Andongo, *Welwitsch 1532* (BM, holotype; LISU, isotype).
M. spithamaea Baker, Trans. Linn. Soc. London, Bot., Ser. 2, 1: 271. 1878. TYPE: Angola, Huila, plains around Humpata and Lopollo, *Welwitsch 1547* (BM, holotype; LISU, isotype).
M. aurantiaca Baker, Fl. Trop. Afr. 7 (addendum): 575. 1898. TYPE: Angola, Malange, *Mechow 303* (B, holotype).
M. kitambensis Baker, Fl. Trop. Afr. 7 (addendum): 575. 1898. TYPE: Angola, Bangala, swamps at Kuango, *Buchner 679* (B, holotype).
M. randii Rendle, J. Bot. 36: 144. 1898. TYPE: Rhodesia, Bulawayo, *Rand s.n.* (BM, holotype).
Ferraria candelabrum (Baker) Rendle, Cat. Afr. Pl. Welw. 2: 27. 1899.
F. andongensis (Baker) Rendle, Cat. Afr. Pl. Welw. 2: 27. 1899.
Moraea malangensis Baker, Bull. Herb. Boissier, sér. 2, 1: 862. 1901. TYPE: Angola, Malange, *Mechow 386* (not seen).
(Other synonyms include *Ferraria welwitschii* Baker and *F. hirschbergii* Bolus.)

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A NEW CLASSIFICATION OF *FICUS*

William Ramírez B.[1]

Abstract

The taxa of *Ficus* are classified on the basis of the specificity and morphology of their symbiotic wasps (Agaonidae), systems of pollination, and morphology and physiology of the figs. The new classification is a modification of Corner's system with the following changes. In subgenus *Ficus*, subsection *Eriosycea* is elevated to sectional rank. Series *Rivulares* and *Pseudopalmae* do not belong to the group of *Blastophaga*-pollinated figs and are transferred to the new *Cerotosolen*-pollinated complex of subgenus *Sycomorus*. Two subsections, *Scabrae* and *Varinga*, are recognized in section *Sycidium*, and series *Phaeopilosae* and subsection *Paleomorphe* are recognized as sections. The subgenus *Sycomorus* is much expanded to include eight sections: *Adenosperma, Neomorphe, Prostratae, Pungentes, Pseudopalmae, Rivulares, Sycocarpus, and Sycomorus.*

The object of this study is to group the taxa of *Ficus* into related groups considering the specificity and morphology of their symbiotic agaonids, the different systems of pollination, as well as the morphology and physiology of the figs.

The last systematic arrangement of *Ficus* was made by Corner (1965) and is summarized in Table 1. A parallel list of the pollinating agaonids (genera or subgenera reported up to now for each fig taxon) is also included. The list of agaonids was taken from Hill (1967) and modified by me. Parallel to the groups of wasps there are columns showing the absence or presence of corbiculae in the wasps (Ramírez, 1974).

The New Classification of *Ficus* and its Pollinators

The proposed classification of *Ficus* is found in Table 3. Modifications are extended only to the level of series.

subgenus *UROSTIGMA*

This group of figs remains as treated by Corner (1965) (Table 1).

Section Urostigma.—The figs are inhabited by *Blastophaga* (group E), which are characterized by the presence of coxal and sternal corbiculae (as in Figs. 3 and 4).

Section Leucogyne.—This section comprises two species. One of them (*F. tsiela*) is pollinated by *Maniella delhiensis*, with coxal and sternal corbiculae (as in Figs. 3 and 4).

Section Conosycea.—The species of this section are pollinated by several groups of wasps. The only *Blastophaga* (*B. arnottiana* and *B. errata*) known from this group of figs have sternal corbiculae and coxal combs. *Ceratosolen megarhopalus* (the Megarhopalus group) and the majority of *Waterstoniella* wasps are characterized by only very rudimentary sternal corbiculae (Figs. 5–6); some

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Waterstoniella (e.g., *W. sundaica* and *W. jacobsoni*) do not have corbiculae (Fig. 2). The other two groups of agaonids (*Eupristina* and *Parapristina*) found in section *Conosycea* have sternal and coxal corbiculae (as in Figs. 3 and 4).

Section Stilpnophyllum.—This section contains only *Ficus elastica* which is pollinated by *Blastophaga clavigera* (*Blastophaga* group B) a wasp with sternal and presumably coxal corbiculae (Wiebes, personal communication).

Section Malvanthera.—This group is unique in that its anthers have two pollen sacs which dehisce with one crescentic or equatorial slit. The section is pollinated by *Pleistodontes* wasps. However, there are apparently several *Pleistodontes* groups pollinating the different groups of *Malvanthera* figs (personal observation).

Pleistodontes imperialis is characterized by sternal and possibly coxal corbiculae while the other known *Pleistodontes* do not possess corbiculae at all. Series *Malvanthereae* is pollinated by wasps without corbiculae (*P. blandus, froggatti, rieki, plebejus,* and *regalis*). The only *Pleistodontes* (*P. inmaturus*) known from series *Cyclanthereae* apparently does not possess corbiculae. For more information on *Pleistodontes* wasps see Wiebes (1963b: 319, Table 1). It is probable that the group *Pleistodontes* as well as its *Ficus* hosts, will have to be reclassified when more is known of both groups.

Section Galoglychia.—This group of figs resembles the last section in the inflexed, not interlocking, apical and internal bracts of the ostiolum (Corner 1959: 376), but it has normal anthers with four pollen sacs. It is pollinated by two main groups of wasps: (a) those with only sternal corbiculae (*Agaon, Allotriozoon* and *Paragaon*) and (b) those with sternal and coxal corbiculae (*Alfonsiella* and *Elisabethiella*).

Section Americana.—According to Corner (1959: 376) this section is closely related to both sections *Urostigma* and *Conosycea.* It is pollinated by *Blastophaga* wasps of the subgenus *Pegoscapus* (Ramírez, 1970) with coxal and sternal corbiculae. However, *P. carlosi* and *P. mariae* (the pollinators of *F. tuerckheimii* in Costa Rica, Mexico and Panama) do not possess coxal corbiculae (Ramírez, 1970).

SUBGENUS *PHARMACOSYCEA*

Corner (1959: 407) considered that the Old World section *Oreosycea* has the same essential characters, and indeed, is with difficulty distinguished from New World *Pharmacosycea* species. However, in the descriptions of the two sections we find very important differences, some of which are pointed out in Table 2.

The Old World species have in the past been referred to the subgenus *Urostigma* where they are out of place, particularly in being independent trees and not banyans or stranglers. The species from New Caledonia have never been properly classified and they are the closest in several respects to the American species. Corner (1959: 407) stated that he divides the subgenus *Pharmacosycea* into two sections, maintaining the geographical distinction for convenience, but that redefinition will be necessary when the American species are better known.

Table 1. Recorded host specificity of Agaonidae (genera and subgenera) to different groups of Ficus. With particular reference to the presence or absence of coxal and sternal corbiculae among different groups of agaonids (modified from Hill, 1967). The systematic breakdown of *Ficus* is taken from Corner (1965).

						Corbiculae		
Subgenus	Section	Subsection	Series	Subseries	Agaonidae	Absent	Sternal	Coxal
Urostigma	*Urostigma*		*Religiosae*		*Blastophaga*		+	+
			Superbae		*Blastophaga*		+	+
			Caulobotryae		*Blastophaga*		+	+
			Orthoneurae		*Blastophaga*		+	+
	Leucogyne				*Maniella*		+	+
	Conosycea	*Conosycea*	*Validae*		*Blastophaga*		+	+ ?
					Megarhopalus group		+	
			Drupaceae	*Drupaceae*	*Eupristina*		+	+
				Indicae	*Eupristina*		+	+
				Zygotricheae	*Waterstoniella*	+		
				Crassirameae	*Eupristina*		+	+
					Blastophaga		+	
					Waterstoniella	+		
					Waterstoniella		+	
		Dictyoneuron	*Glaberrimae*					
			Dubiae					
			Subvalidae		*Waterstoniella*	+		
			Perforatae					
		Benjamina	*Benjamineae*		*Eupristina*		+	+
			Callophylleae		*Parapristina*		+	+
	Stilpnophyllum				*Blastophaga*		+	?
	Malvanthera		*Malvanthereae*	*Eubracteatae*	*Pleistodontes*	+		
				Malvanthereae	*Pleistodontes*	+		
				Platypodeae	*Pleistodontes*		+	+ ?
				Hesperidiiformes	*Pleistodontes*	+		
			Cyclanthereae		*Pleistodontes*	+		
	Galoglychia				*Agaon*		+	
					Paragaon		+	
					Allotriozoon		+	
					Elisabethiella		+	+
					Alfonsiella		+	+
	Americana				*Pegoscapus*		+	+

Table 1. (Continued)

Subgenus	Section	Subsection	Series	Subseries	Agaonidae	Corbiculae Absent	Corbiculae Sternal	Corbiculae Coxal
Pharmacosycea	*Oreosycea*		*Vasculosae*	*Albipilae*				
				Vasculosae	*Dolichoris*		+	+
					Blastophaga		+	+
			Nervosae		*Blastophaga*		+	+
			Austrocaledonicae		*Blastophaga*		+	+
	Pharmacosycea				*Tetrapus*	+		
Ficus	*Ficus*	*Ficus*	*Rivulares*					
			Pseudopalmeae		*Ceratosolen*		+	
			Sinosyceae					
			Cariceae		*Blastophaga*	+		
			Erythrogyneae		*Blastophaga*	+		
			Podosyceae	*Podosyceae*	*Blastophaga*	+		
				Basitepalae				
		Eriosycea	*Eriosyceae*	*Eriosyceae*	*Blastophaga*		+	
				Trichosyceae				
				Dehiscentes				
				Cuneifoliae				
			Auratae	*Auratae*				
				Monandreae				
	Rhizocladus							
			Plagiostigmaticae	*Plagiostigmaticae*	*Blastophaga*	+		
				Pogonotropheae				
			Ramentaceae	*Pantonianae*				
				Balanotae				
				Irritantes				
				Ramentaceae				
				Excavatae				
				Araneosae				
			Distichoideae					
			Distichae					

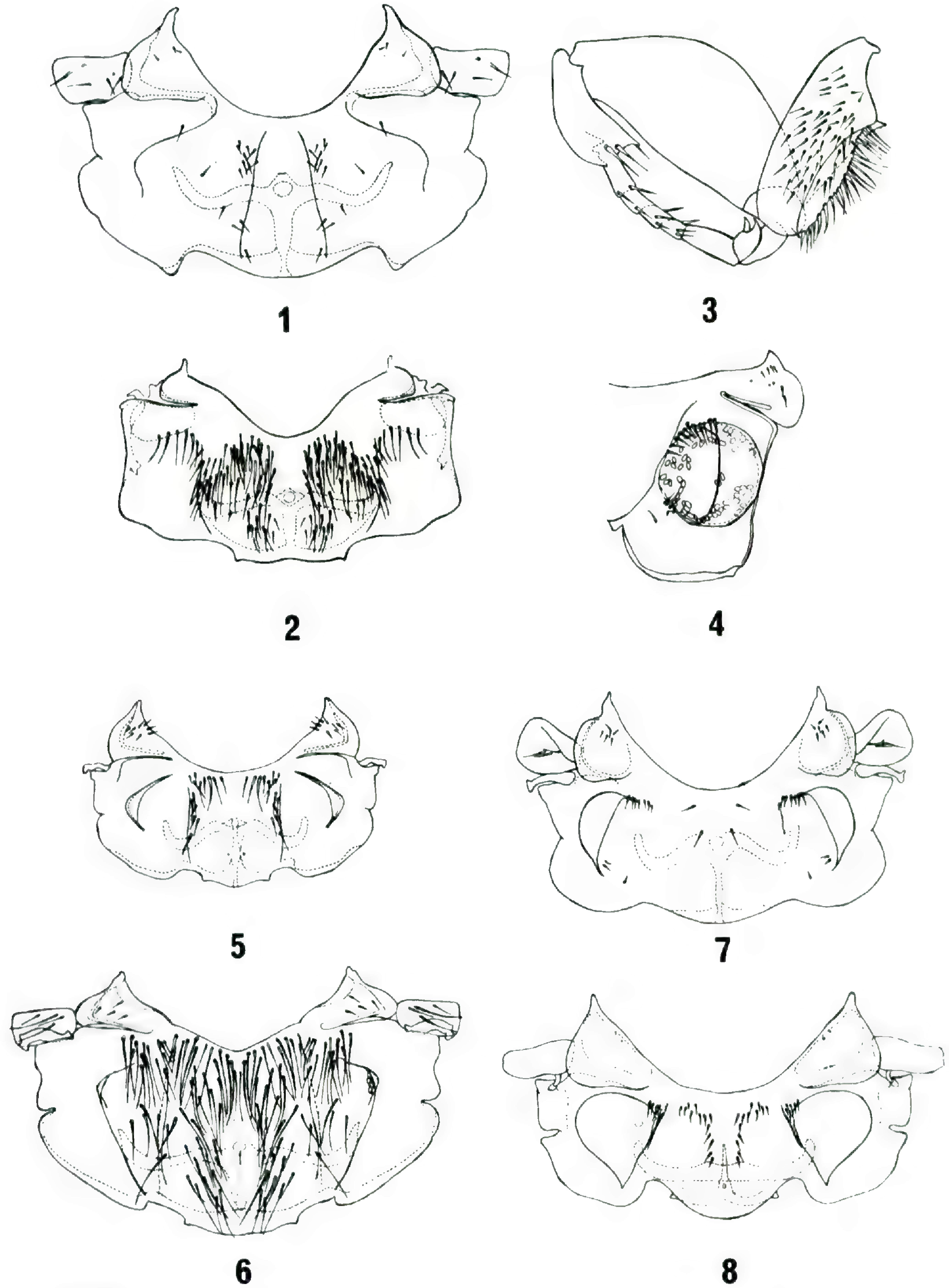
TABLE 1. (Continued)

Subgenus	Section	Subsection	Series	Subseries	Agaonidae	Corbiculae Absent	Corbiculae Sternal	Corbiculae Coxal
			Trichocarpeae					
	Kalosyce				*Blastophaga*	+		
			Apiocarpeae					
			Punctatae					
				Punctatae				
				Ruginerviae				
	Sinosycidium							
Ficus	*Sycidium*	*Sycidium*	*Prostratae*		*Ceratosolen*		+	
			Pungentes		*Ceratosolen*		+	
			Phaeopilosae[2]		*Blastophaga*[2]		+	
			Copiosae		*Blastophaga*		+	
			Scabrae		*Blastophaga*		+	
		Varinga					+	
			Heterophylleae					
			Cyrtophylleae					
			Exasperatae		*Blastophaga*		+	
		Paleomorphe	*Pallidae*		*Liporrhopalum*		+	
			Subulatae		*Liporrhopalum*		+	
			Cuspidatae		*Liporrhopalum*		+	
			Minutuliflorae		*Liporrhopalum*		+	
			Fibrosifoliae		*Liporrhopalum*		+	
	Adenosperma		*Amphigenae*		*Ceratosolen*		+	
			Hypogenae		*Ceratosolen*		+	
	Neomorphe				*Ceratosolen*		+	
			Auriculatae		*Ceratosolen*		+	
			Variegatae	*Variegatae*	*Ceratosolen*		+	
				Laciniatae				
	Sycocarpus	*Auriculisperma*	*Cynaroides*					
			Theophrastoides		*Ceratosolen*		+	
			Vitienses					
		Dammaropsis						
		Papuasyce			*Ceratosolen*		+	

TABLE 1. (Continued)

Subgenus	Section	Subsection	Series	Subseries	Agaonidae	Corbiculae Absent	Corbiculae Sternal	Corbiculae Coxal
		Lepidotus						
		Macrostyla						
		Sycocarpus	*Longetuberculatae*					
			Tuberculi-fasciculatae					
				Praestantes				
				Calopilinae	*Ceratosolen*		+	
				Congestae	*Ceratosolen*		+	
				Hispidae	*Ceratosolen*		+	
				Axillares	*Ceratosolen*		+	
				Fulvidulae	*Ceratosolen*		+	
				Geocarpicae				
				Tuberculi-fasciculatae				
Sycomorus					*Ceratosolen*		+	

[a] At present these species are placed in *Blastophaga*, but they show different degrees of intergradating with *Ceratosolen*, especially in the females (Hill, 1967).



FIGURES 1–8.—1. Mesosternum without corbiculae of *Blastophaga psenes*, the pollinator of the edible fig.—2. Mesosternum of *Blastophaga* (*Waterstoniella*) *sundaica*, a wasp without corbiculae but with abundant bristles which are probably used to carry pollen.—3. Front leg of *Maniella delhiensis* with coxal corbicula.—4. Right side of mesosternum of *Blastophaga* (*Pegoscapus*) *cumanensis* showing corbicula and some pollen in place.—5. Mesosternum of *Blastophaga* (*Waterstoniella*) *sundaica* with incipient corbiculae.—6. Mesosternum of *Ceratosolen megarhopalus* (the Megarhopalus group), right corbicula with some pollen.—7. Mesosternum of *Blastophaga javana* (*Blastophaga* group B) with developed open corbiculae.—8. Mesosternum of *Liporrhopalum mindanaensis* with closed corbiculae as in *Ceratosolen*.

TABLE 2. Presence or absence of some characters in the two sections of subgenus *Pharmacosycea.*

Section	Figs Single	Ostiolum Crateriform	Ovary with a Red Mark	Pachycaulous Trees	Anthers Numerous	Pollen Exposed at Male Phase
Pharmacosycea	+	+	+	–	+	+
Oreosycea	–	–	–	+	–	–

Corner (1967: 40) noted that the new look brought into the subgenus *Pharmacosycea* by the plants from New Caledonia is the brown hairiness, sometimes almost furriness, of twig, leaf, and fig, coupled with the rosettes of large leaves, the many-veined obovate lamina with cordate base and short petiole, and the large size of the fig. All of these characters are more or less primitive and pachycaul signs in *Ficus*. Section *Pharmacosycea* in the New World does not present all the pachycaulous characters mentioned by Corner (1967) for some Old World *Oreosycea.*

In order to explain the presence of pharmacosyceous figs in both the Old and New World, Corner (1967: 41) postulated that there must have been a land connection with tropical Africa such as is suggested by the great extension of the 4,000 mile line to the west of Peru. In 1967 he further stated that this connection is demanded by other moraceous genera such as *Antiaris, Antiaropsis, Sparattosyce* and *Trophis*, as well as by the monocotyledons *Dianella, Heliconia* and *Spathiphyllum* in very diverse families.

Two hypotheses to explain the presence of *Pharmacosycea* in the Old and New Worlds are: (a) Sections *Pharmacosycea* and *Oreosycea* do not belong to the same subgeneric taxon and their species are more or less similar because of convergence. If this is true, each should be elevated to the subgeneric level, forming biological units separated geographically and by their respective pollinators, New World *Pharmacosycea* being the host of *Tetrapus* wasps (without corbiculae) and Old World *Oreosycea* of *Blastophaga* (*Blastophaga* group F) and of *Dolichoris vasculosae* (both with coxal and sternal corbiculae). (b) Sections *Pharmacosycea* and *Oreosycea* belong to the same subgeneric category, but section *Pharmacosycea* migrated to the New World before the agaonids evolved corbiculae. This line of thought would agree with the ideas of Corner (1967: 53), although not demonstrating the particular land connection that he postulated.

SUBGENUS *FICUS*

In the new classification the subsections *Ficus* and *Eriosycea* are elevated to sectional rank as suggested by Corner (1959: 417). The series *Rivulares* and *Pseudopalmeae* are not considered to belong to the group of *Blastophaga*-pollinated figs and are transferred to the new *Ceratosolen*-pollinated complex (the subgenus *Sycomorus*, Table 3). Corner (1969b: 326) stated that *F. pseudopalma* and *F. rivularis* (two Philippine species) differ from the rest of section *Ficus* and from each other markedly enough to require separate taxonomic series (Table

TABLE 3. Proposed classification of the genus *Ficus* considering the specificity and morphology of its symbiotic agaonids, the different systems of pollination, as well as the morphology and physiology of the figs; with a list of the agaonid pollinators (modified from Hill, 1967) of each group, and the presence or absence of corbiculae.

				Corbiculae		
Subgenus	Section	Subsection	Agaonidae	Absent	Sternal	Coxal
Urostigma	*Urostigma*		*Blastophaga* Group E		+	+
	Leucogyne		*Maniella*		+	+
	Conosycea	*Conosycea*	*Blastophaga*		+	+ ?
			Megarhopalus Group		+	
			Eupristina		+	+
			Waterstoniella	+		
			Waterstoniella		+	
		Dictyoneuron	*Waterstoniella*	+		
			Eupristina		+	+
		Benjamina	*Parapristina*		+	+
	Stilpnophyllum		*Blastophaga clavigera* (=*Blastophaga* Group G)		+	+ ?
	Malvanthera		*Pleistodontes*	+		
			Pleistodontes		+	+ ?
	Galoclychia		*Agaon*		+	
			Alfonsiella		+	+
			Allotriozoon		+	
			Elisabethiella		+	+
			Paragaon		+	
	Americana		*Pegoscapus*		+	+
Pharmacosycea	*Oreosycea*		*Blastophaga* Group F		+	+
			Dolichoris		+	+
	Pharmacosycea		*Tetrapus*	+		
Ficus	*Ficus*		*Blastophaga* Group A	+		
	Rhizocladus		*Blastophaga* Group A	+		
	Kalosyce		*Blastophaga* Group A	+		
	Sinosycidium[a]					
	Eriosycea		*Blastophaga* Group B		+	
	Sycidium	*Scabrae*	*Blastophaga* Group B		+	
		Varinga	*Blastophaga* Group B		+	
	Phaeopilosae		*Blastophaga* Group C		+	
	Paleomorphe	*Paleomorphe*	*Liporrhopalum*		+	
		Copiosae	*Blastophaga* Group D		+	

TABLE 3. (Continued)

Subgenus	Section	Subsection	Agaonidae	Corbiculae Absent	Corbiculae Sternal	Corbiculae Coxal
Sycomorus	*Adenosperma*		*Ceratosolen*		+	
	Neomorphe		*Ceratosolen*		+	
	Prostratae		*Ceratosolen*		+	
	Pugentes		*Ceratosolen*		+	
	Pseudopalmeae		*Ceratosolen*		+	
	Rivulares[b]				+	
	Sycomorus		*Ceratosolen*		+	
	Sycocarpus		*Ceratosolen*		+	

[a] Probably pollinated by a wasp of *Blastophaga*, Group A.
[b] Probably pollinated by a *Ceratosolen* wasp.

1). Wiebes (1963a: 101, 104) indicated that the pollinator of *F. pseudopalma* (*C. bakeri*) has aberrant characters for the genus *Ceratosolen*, but appears related to the *C. abnormis* and *C. armipes* groups (pollinators of figs of section *Sycocarpus*).

Sections Kalosyce and Rhizocladus.—These two sections are left in the taxonomic position given them by Corner (1965). They form two well-defined groups pollinated by *Blastophaga* (*Blastophaga* group A) wasps without corbiculae (Fig. 1). The pollinators of these two groups of figs are quite similar to the ones found with section *Ficus* (Table 3). These two sections are associated by their pollinators. Corner (1960: 3), however, suggested that sections *Kalosyce* and *Rhizocladus* might be considered to form a fifth subgenus.

Section Sinosycidium.—This section is left in the same taxonomic position given by Corner (1960: 24). It has a single species (*F. tsiangii*). Because of its dispersed diandrous flowers and the slightly bifid stigmata of the female flowers, I consider this section to be related to section *Ficus* (as in Table 3), although the ramiflorous bracteate receptables are like those which occur in sections *Sycidium*, *Sycocarpus* and *Adenosperma* according to Corner (1960: 24–25). The pollinator of *F. tsiangii* is not known, but it could be a *Blastophaga* without corbiculae (as in Fig. 1) as those of *Blastophaga* group A.

Section Sycidium.—In the new classification this group has two subsections, *Scabrae* and *Varinga*. These groups are related by their pollinators of the *Blastophaga* group B, which are characterized by their open sternal corbiculae (Fig. 7).

Sections Phaeopilosae and Paleomorphe.—The series *Phaeopilosae* and subsection *Paleomorphe* (both sensu Corner, 1965) are elevated to sectional rank. *Phaeopilosae* is pollinated by *Blastophaga* group C with closed sternal corbiculae (Fig. 9). *Paleomorphe* has two subsections, *Paleomorphe* being pollinated by *Liporrhopalum* with closed sternal corbiculae (Fig. 8) and *Copiosae* (series *Copiosae*, sensu Corner, 1965) by *Blastophaga* group D having closed sternal corbiculae (as in Fig. 9).

SUBGENUS *SYCOMORUS*

In the new classification the subgenus *Sycomorus* is expanded and comprises eight sections: *Adenosperma, Neomorphe, Prostratae, Pungentes, Pseudopalmeae, Rivulares, Sycocarpus* and *Sycomorus* (Table 3). Of these sections, *Adenosperma, Neomorphe* and *Sycocarpus* were considered by Corner (1965) as sections of the subgenus *Ficus*; *Prostratae* and *Pungentes* as series of subsection *Sycidium*; *Pseudopalmeae* and *Rivulares* as series of subsection *Ficus*.

All the sections included here in *Sycomorus*, excepting *Rivulares*, are known to be pollinated by *Ceratosolen* wasps. The pollinator of *Ficus rivularis* (the only species of section *Rivulares*) is not known, but I suspect this species to be pollinated by a *Ceratosolen* with a short ovipositor and closed sternal corbiculae. All the dioecious sections (*Adenosperma, Neomorphe, Prostratae, Pungentes, Pseudopalmeae* and *Sycocarpus*) are inhabited by *Ceratosolen* wasps with short ovipositors. Nevertheless, Corner (1965: 85) included in section *Sycocarpus* (subsection *Papuasyce*) the species *F. microdictya* (of New Guinea) which has the perianth similar to that of *Sycocarpus*, but is monoecious like *Sycomorus*[2], which does not occur in New Guinea (Corner, 1958: 31, personal communication). Section *Sycomorus* is a monoecious group pollinated by *Ceratosolen* with long ovipositors.

RELATIONSHIPS AMONG GROUPS OF FIGS INCLUDED IN SUBGENUS *SYCOMORUS*

SECTION *ADENOSPERMA*

This section aligns with the unistaminate sections *Sycidium* and *Sycocarpus*, which differ in the form of the seed if not in that of the flower (Corner, 1969b: 320). The section is related to section *Sycocarpus*, subsection *Auriculisperma*, of the Solomon Islands, and connects with the origin of section *Ficus* through the Philippine species *F. pseudopalma* and *F. rivularis* (Corner, 1969b: 319).

SECTION *NEOMORPHE*

Corner (1967: 51) stated that this section has much in common with the subgenus *Sycomorus*. *Neomorphe* may have come from the stock of *Adenosperma* on the Melanesian Foreland, and this stock may have been connected with that of *Sycomorus*, so that *Neomorphe* is an eastern parallel of it (Corner, 1967: 51). *Neomorphe* must be divided into two series (Table 1), *Variegatae* and *Auriculatae*, which show alliance with the subgenus *Sycomorus* in the first case and section *Sycocarpus* in the second. Series *Variegatae* can be divided, likewise, into two subseries. The first Corner (1965: 32–33) called subseries *Laciniatae*. It has tepals characteristic of subgenus *Sycomorus*, but it is further removed geographically from the African subgenus *Sycomorus* (Corner, 1967). The second, subseries *Variegatae*, has only two species, *F. variegata* and *F. viridicarpa*. *Ceratosolen striatus* (=*C. appendiculatus*), an agaonid collected from *F. variegata* in Java, was illustrated by Grandi (1917:

[2] *Ficus pritchardii*, a monoecious fig, also belongs to *Sycocarpus* (Corner, 1970).

Fig. XII, 6) as a wasp with a long ovipositor like the wasps found in section *Sycomorus* (as in Table 3).

Neomorphe as well as subgenus *Sycomorus* of Corner (1965) are pollinated by *Ceratosolen* wasps which are apparently related. Wiebes (1963a: 104) reported that the species of the *Ceratosolen appendiculatus* group live in the receptables of section *Neomorphe* and subgenus *Sycomorus* (sensu Corner, 1965), and one species is known from series *Prostratae*. The occurrence of a group of such closely related species of *Ceratosolen* in the figs of both dioecious *Neomorphe* and monoecious *Sycomorus* would suggest that the floral characters in which *Neomorphe* is close to *Sycomorus* are more important than the distribution of the flowers in the receptacles. A parallel is found in *F. microdictya*, which is a monoecious species in the dioecious *Sycocarpus*[3] (Wiebes, 1963a: 104).

SECTIONS *PROSTRATAE* AND *PUNGENTES*

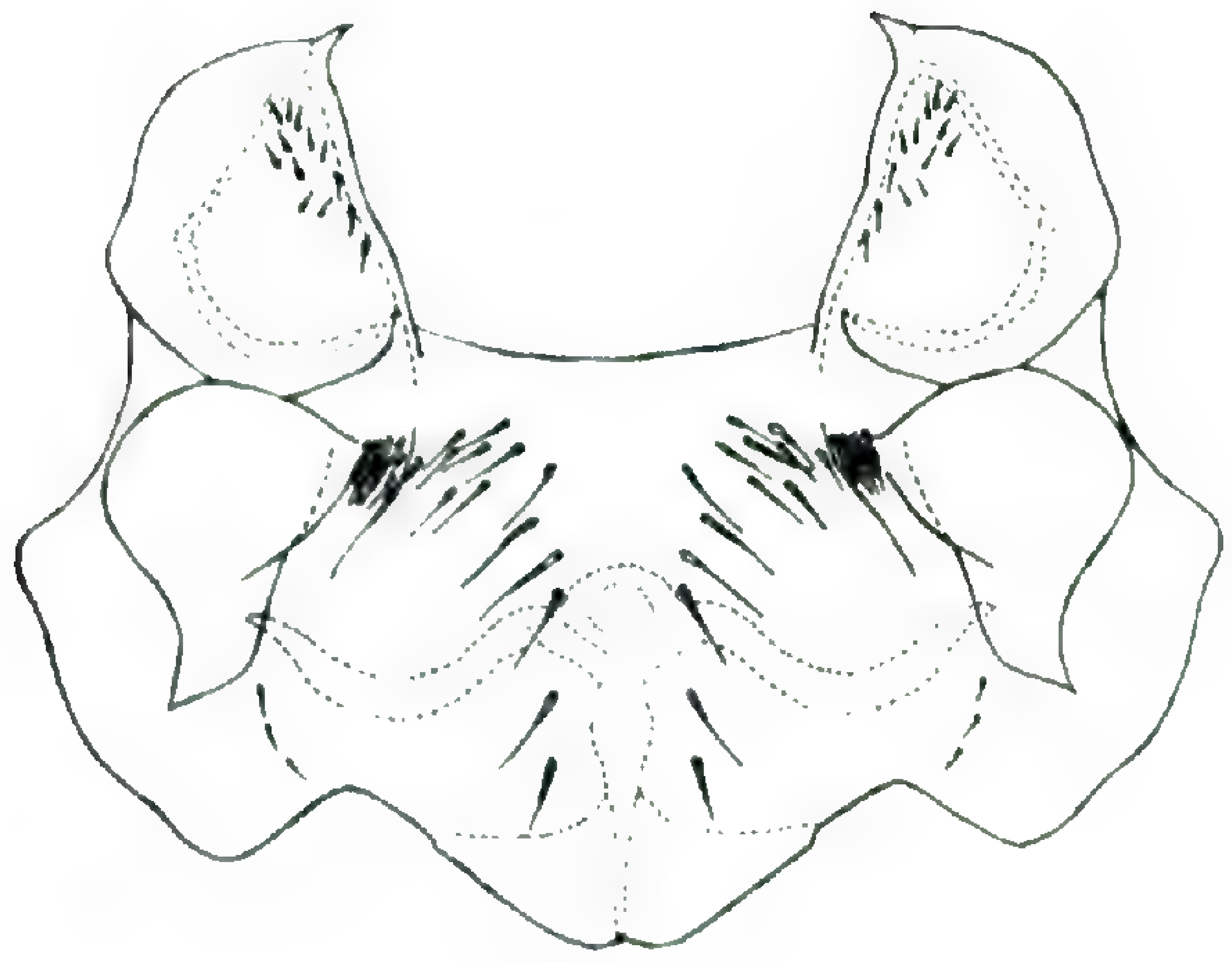
These sections are also pollinated by *Ceratosolen* wasps. Corner (1965) considers them to be two series of section *Sycidium*. According to Wiebes (1963a: 102), the greater part of the Indomalayan and Papuan species of *Ceratosolen* live in the sections *Neomorphe* and *Sycocarpus*, but some are known from *Prostratae* and *Pungentes*, two series of *Sycidium* (sensu Corner, 1965). These series have usually been placed in section *Sycocarpus* and only recently have been assigned to *Sycidium* (Wiebes, 1963a). Botanically these two series point to a common ancestor which would combine *Sycidium* with *Sycocarpus* and *Sycomorus*, including *Neomorphe* (Corner, 1958: 31). In the opinion of Wiebes (1963a: 102) the wasps from the series *Prostratae* connect those from the section *Neomorphe* with those of the subgenus *Sycomorus*, and the wasps from the series *Pungentes* appear to be related to the wasps from the section *Sycocarpus*. According to Corner (1959: 444), series *Prostratae* relates with section *Ficus* but habit and convenience place it in *Sycidium*.

SECTIONS *PSEUDOPALMEAE* AND *RIVULARES*

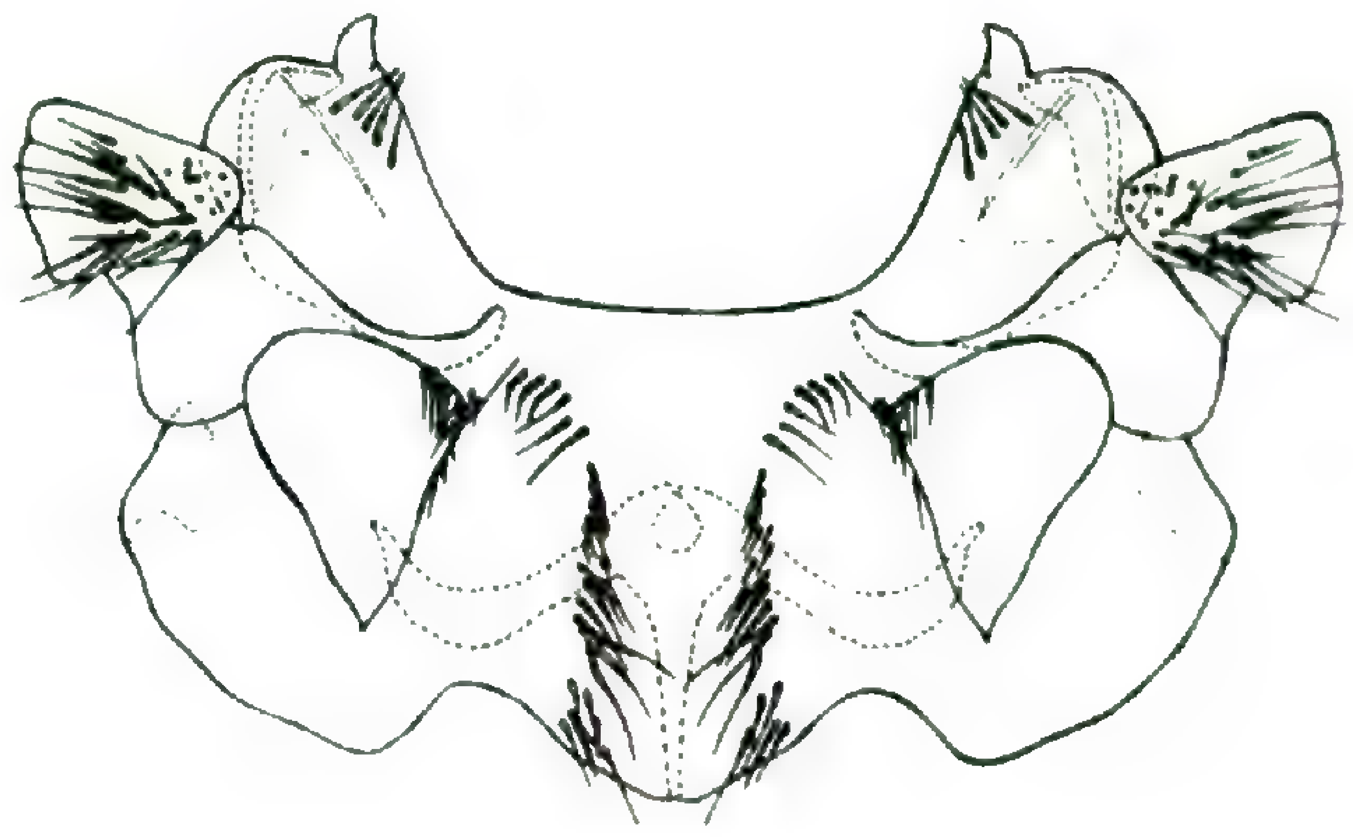
Each of these taxa has a single species. Corner (1965) included them as two series of the subgenus *Ficus*. Both species are found in the Philippines. *Ficus rivularis* is an advanced leptocaul shrub with lanceolate leaves, distinguished in section *Ficus* by the gamophyllous perianth with distinct tepal lobes, compressed auriculiform seed, and the more or less gynobasic style in the female flower. The perianth is intermediate between that of section *Ficus* and *Sycocarpus*. In perianth, style and seed, *F. rivularis* agrees with *Adenosperma*; it appears as a relic, fitting no section of the ancestral line of section *Ficus* from which those of *Auriculisperma* and *Adenosperma* diverged (Corner 1969b: 328).

Ficus pseudopalma connects as a pachycaul with *F. dammaropsis* (section *Sycocarpus*, subsection *Auriculisperma*) of New Guinea, and thus, with section *Adenosperma*. It connects also with the ancestry of the *F. deltoidea* complex (section *Ficus* series *Erythrogyneae*) and has the three tepals of section *Ficus*

[3] *Ficus pritchardii* (a monoecious fig) also belongs to *Sycocarpus*.



9



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FIGURES 9–10.—9. Mesosternum of *Blastophaga jacobsi* (*Blastophaga* group C) with closed sternal corbiculae.—10. Mesosternum of *Ceratosolen pilipis* with closed corbiculae.

(Corner, 1969b: 326). *Ceratosolen bakeri* is the pollinator of *F. pseudopalma*. This wasp appears to be related to the *C. abnormis* and the *C. armipes* groups. *Ficus pseudopalma* was classified in section *Ficus* because of its bistaminate male flowers, but it does show some relationship with *F. dammaropsis* (section *Sycocarpus*), the host of *C. abnormis* (Wiebes, 1963a: 101).

SECTION *SYCOCARPUS*

This group of *Ficus* is mostly dioecious; however, *F. microdictya* and *F. pritchardii* are monoecious. It is pollinated by *Ceratosolen* wasps with short ovipositors, but the ovipositors of the pollinators of *F. microdictya* and *F. pritchardii* are probably much longer than the abdomens. The chief character of the section is the entirely gamophyllous perianth. In the male flower the perianth is saccate and covers one, or less often, two stamens (Corner 1960: 38). For the relationship of the pollinators of *Sycocarpus* with the pollinator of *F. pseudopalma* and those of section *Nemorphe*, see under sections *Pseudopalmeae* and *Neomorphe*. See also under section *Adenosperma*.

SECTION *SYCOMORUS*

In the new classification, this group contains all the monoecious figs included in the subgenus *Sycomorus* of Corner (1965). It is pollinated by *Ceratosolen* wasps with long ovipositors.

Galil (1973) noted that in spite of numerous structural differences between the syconia of the dioecious *F. fistulosa* (section *Sycocarpus*) and the monoecious *F. sycomorus* (section *Sycomorus* sensu Ramírez, 1974) which belong to different subgenera of *Ficus*, namely *Ficus* and *Sycomorus* (sensu Corner, 1965) respectively, the two have several biological features in common. In both, the pollinating wasps are species of *Ceratosolen* which behave very similarly in relation to the figs, and such likeness in behavior indicates that physiological conditions within the figs are probably also similar in both cases.

Characters of the Subgenus *Sycomorus*

Corner (1967: 51) stated that *Sycomorus*, *Sycocarpus*, *Adenosperma*, *Neomorphe*, and two series of *Sycidium* (*Prostratae* and *Pungentes*) are distinguished by having *Ceratosolen* as pollinating insects. Despite their differences, he suggests it may be necessary to combine them in the subgenus *Sycomorus* in contrast with the remainder of the subgenus *Ficus* pollinated by *Blastophaga*.

The newly defined subgenus *Sycomorus* is characterized by the following characters: *Male flowers*: (a) in 1 or 2 (in some cases 3) ostiolar rings; (b) few per fig; (c) usually without pistillode; (d) perianth with free petals, gamophyllous or utriculate; (e) mostly sessile; (f) usually with only one or two stamens (few species with three). *Anthers*: (a) enfolded by the perianth; (b) usually small; (c) pollen not exposed at male phase. *Female flowers*: (a) stigma simple; (b) styles usually short excepting those of section *Sycomorus* and of *F. microdictya* and *pritchardii*[4]. *Syconia*: (a) with internal bristles; (b) helicoidal ostiolar entrance with several (more than three) interleafing superficial bracts; (c) dioecious (excepting section *Sycomorus* and *F. microdictya* and *pritchardii*; (d) ostiolum usually does not open at male phase. *Leaf*: (a) stomata usually superficial; (b) leaf not coriaceous; (c) plicate in bud. *Trees*: independent, not epiphytic. *Pollinators*: *Ceratosolen* wasps which are characterized by closed sternal corbiculae (as in Fig. 10), and coxal combs, and which collect the pollen from detached anthers cut by the males (Galil, 1973); short ovipositors (except the *Ceratosolen* wasps of section *Sycomorus* and *F. microdictya* and *pritchardii*) and by the ability of the male to perforate the fig in order to gnaw an exit that allows the females to escape. The males in all species probably cut the stamens before the females emerge from the galls (Galil, 1973).

The figs of sections *Adenosperma*, *Sycocarpus*, and *Sycomorus* are parasitized by *Eukoebelea* wasps (tribe *Sycophagini*, Hill, 1967: 92), while the species of section *Sycomorus* are inhabited by *Sycophaga* wasps (tribe *Sycophagini*, Hill, 1967: 92).

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[4] Corner (1970: 383) suggested that subsection *Papuasyce* (of section *Sycocarpus*), to which *F. itoana*, *microdictya* and *pritchardii* belong, should become a fifth subgenus as a monoecious group distinct from subgenus *Ficus* but with *F. itoana* as the dioecious product.

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STUDIES IN BIGNONIACEAE 25: NEW SPECIES AND COMBINATIONS IN SOUTH AMERICAN BIGNONIACEAE[1]

Alwyn H. Gentry[2]

Abstract

Five new species of South American Bignoniaceae are described—*Anemopaegma granvillei* A. Gentry, *Arrabidaea ornithophila* A. Gentry, *Cuspidaria octoptera* A. Gentry, *Memora cristicalyx* A. Gentry, and *Tabebuia catarinensis* A. Gentry—and two new combinations—*Lundia virginalis* var. *nitidula* (DC.) A. Gentry and *Memora imperatoris-maximilianii* (Wawra) A. Gentry—are made.

Anemopaegma granvillei A. Gentry, sp nov.

Frutex scandens; sine pseudostipulis vel consociebus glandularum in nodis inter petiolos; folia 2-foliolata, foliolis oblongo-ellipticis, infra omnino puberulis; inflorescentia axillaris, racemosa, puberula; flores calyce cupulato, corolla lutea, tubo extus glabro, ovario ovoideo, minute lepidoto, ad basim non contracto; fructus ignotus.

Vine; branchlets finely but prominently striate, elenticellate, puberulous, without interpetiolar glandular fields; pseudostipules (only 1 seen) subulate, 4 mm by 1 mm. Leaves 2-foliolate, sometimes tendrillate (tendril tip not seen); leaflets (ovate-)oblong-elliptic, shortly and obtusely acuminate, rounded or truncate at the base, 10–15 cm long, 4.5–6.5 cm wide, chartaceous, puberulous throughout beneath with rather scattered erect trichomes, above puberulous only along the main veins, the secondary veins looped and connecting several mm from the margins, not very prominent nor strongly ascending, drying olive, glossy above, dull below. Inflorescence a contracted axillary raceme, densely tannish puberulous; pedicels subtended by linear 2–3 mm long bracts. Flowers with the calyx cupular, asymmetrically truncate, 7–10 mm long, 7–8 mm wide, puberulous at the base and around the margin, with fields of plate-shaped glands in the upper half; corolla tube pale to lemon yellow, the lobes pale yellow, tubular-campanulate, ca. 5 cm long, the tube 3.5–4 cm long, the lobes ca. 1 cm long, the tube glabrous outside, the lobes glandular-lepidote with ciliate margins, large glands absent below the lobes; stamens didynamous; ovary (in bud) ovoid, longitudinally ridged, minutely lepidote, not contracted at the base; disc large, patelliform, 2 mm long, 3 mm wide. Fruit unknown.

Type: French Guiana. Riviere Petite Ouaqui, végétation ripicole verse l'embouchure de la crique Carbet Brûlé, 27 July 1973, *de Granville 1935* (CAY, holotype and isotype; MO, fragments and photocopy).

The combination of glabrous corolla tube and puberulous leaves indicates affinity with *A. puberulum* (Seib.) Miranda which belongs to the *A. grandifolium* (Jacq.) Merrill & Sandw. complex. However, all species of this complex

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differ in having more prominently lenticellate branchlets and much more prominent and strongly ascending secondary venation. Inflorescence bracts of *A. puberulum* and its relatives are also smaller and less prominent, and leaves are relatively ovate, never as oblong as in the new species. Of the other pubescent-leaved *Anemopaegma* species, *A. villosum* A. Gentry, *A. rugosum* (Schlecht.) Sprague, *A. goyazense* K. Schum., and *A. velutinum* Mart. ex DC. have prominently lepidote corolla tubes. The former two also differ in possessing foliaceous pseudostipules, the latter two have more densely pubescent 3-foliolate leaves. Only two conspicuously pubescent-leaved species have glabrous corolla tubes—*A. hilarianum* Bureau & K. Schum. has more pubescent, smaller, ovate leaves and a paniculate inflorescence; *A. brevipes* S. Moore, which may be the closest relative of *A. granvillei*, has foliaceous pseudostipules, a shorter calyx and smaller leaflets which are much more densely puberulous beneath.

Arrabidaea ornithophila A. Gentry, sp. nov.—FIG. 1.

Frutex scandens; interdum consociebus glandularum in nodis inter petioles; folia trifoliolata, foliolis elliptico-oblongis; inflorescentia floribus in panicula terminali dispositis; calyx tubulosus, bilabiatus, puberulus; corolla rosea, tubulosa; stamina subexserta, thecis pendulis; ovarium oblongum, lepidotum; discus annulatim pulvinatus; capsula linearis.

Liana; branchlets terete, puberulous, with or without inconspicuous interpetiolar glandular fields; pseudostipules lacking. Leaves 3-foliolate (sometimes simple in part); leaflets elliptic-oblong, rounded to acuminate at the apex, rounded at the base, 7–21 cm long, 4–10 cm wide, chartaceous, above minutely lepidote, otherwise glabrous or with a few inconspicuous trichomes along the main vein, below densely puberulous, drying dark above, light gray below; petiolules 1–4 cm long; petioles 2.5–6 cm long, lepidote and puberulous. Inflorescence a terminal panicle, its branchlets densely puberulous with short glandular trichomes and longer nonglandular trichomes. Flowers with the calyx tubular, bilabiate, 10–13 mm long, 5–7 mm wide, the lobes almost 2 mm long, densely pubescent with conspicuously reddish glandular and eglandular trichomes; corolla cherry red, tubular, 2.3–2.5 cm long, 0.4–0.5 cm wide at the mouth of the tube, the tube 1.9–2.1 cm long, the lobes 2–3 mm long, densely puberulous outside, inside very densely pilose with exceedingly long (several mm) tangled trichomes in the upper part of the tube, these completely filling the throat, less densely pilose with shorter trichomes below, villous at the level of stamen insertion; stamens didynamous, inserted 3–4 mm from the base of the corolla tube, subexserted, the anther thecae subparallel, 3 mm long (including connective), joined for the upper 1.4–2 mm, slightly divergent basally, the connective extended 1.4 mm beyond the point of attachment, the filaments 1.6–1.8 cm long, the staminode 4 mm long; pistil ca. 2 cm long, the ovary oblong, tapering slightly towards the top, 2 mm long, 0.8 mm wide, densely glandular lepidote; disc pulvinate, 1 mm long, 2–2.5 mm wide. Fruit linear, compressed, the apex and base subacute, ca. 20 cm long, drying dark.

TYPE: BRAZIL. PARA: Distrito Acará, Thomé Assú, Pão Vermelho, 50 m, border woods in sun, vine climbing small trees, cherry red flower, occasional, 3 Aug. 1931, *Y. Mexia 6041* (MO, holotype; NY, US, isotypes).

FIGURE 1. *Arrabidaea ornithophila* A. Gentry.—A. Inflorescence; ×3/5.—B. Leaves; ×3/5. [After *Mexia 6041* (MO).]

Additional collections examined: BRAZIL. MARANHÃO: Km 374 Belém-Brasilia, cipo sobre árvores, flores vermelhas, 26 Aug. 1960, *Oliveira 1046* (IAN). AMAPA: Santa Patricia, margem esquerda do Rio Jarí, 160 m, 13 Mar. 1970, *Silva 2971* (IAN). PARA: Km 32, Belém-Brasilia highway, liana, corolla red, 27 Aug. 1964, *Prance & Silva 58902* (NY). Km. 289–293, Belém-Brasilia, cipo sobre árvores, flores vermelhas em forma de tubo, frutos em vagem compridos e chatos, 31 July 1960, *Oliveira 945* (IAN). Estrada Belém-Brasilia, cipo, flores vermelhas, vistosas ornamental, May 1960, *Froes 34938* (IAN). Rodovia Belém-Brasilia, km 92, flores vermelhas, 21 Aug. 1959, *Kuhlmann & Jimbo 78* (IAN). Km 167–173 da Estrada Belém-Brasilia, flores vermelhas em cachos, 25 Apr. 1960, *Oliveira 549* (IAN). Km 243–239 da Rodovia Belém-Brasilia, 8 July 1960, *Oliveira 878* (IAN). Region do Rio Jarí, estrada de Monte Dourado ao Mungaba, 27 June 1968, *Oliveira 4681* (IAN, NY); 2 July 1968, *Oliveira 4739* (IAN, NY); 10 June 1968, *Silva 2149* (IAN). Rio Jarí, Planalto de Monte Dourado, 16 June 1968, *Oliveira 4548* (IAN, NY); 2 Oct. 1968, *Silva 1084* (NY). Rio Jarí, serra de Monte Dourado, 140 m, 10 Nov. 1967, *Oliveira 3604* (IAN, NY); 13 Nov. 1967, *Oliveira 3524* (IAN); 18 June 1970, *Silva 3227* (IAN).

The closest relatives of this very distinct, presumably hummingbird-pollinated, species are *Arrabidaea trailii* Sprague and *Fridericia speciosa* Mart. *Arrabidaea trailii* has a similar (but smaller) tubular red corolla with subexserted (but much smaller and with a minute connective) anthers and gray-drying (but never simple) leaves with densely puberulous undersurfaces. The calyx of *A. trailii* is smaller, subtruncate, and evenly 5-denticulate. The flower and calyx of *A. ornithophila* are even more similar to those of *Fridericia speciosa* except that the calyx of *Fridericia* is somewhat inflated and conspicuously 5-ridged. The anthers of *Fridericia* are included and the thecae divergent. The new species is so clearly intermediate between *Arrabidaea trailii* and *F. speciosa* that its existence seriously weakens the case for retention of monotypic *Fridericia* as a distinct genus.

Cuspidaria octoptera A. Gentry, sp. nov.

Frutex scandens; ramuli teretes, sine pseudostipulis, consociebus glandularum in nodis inter petiolos; folia 3-foliolata vel 2-foliolata, interdum cum cirrho, foliolis ovatis vel ellipticis, infra sparsim puberulis saltem nervisequentibus; inflorescentia paniculata, bracteata; flores calyce cupulato, 5-denticulato, corolla tubulo-infundibuliformi, extus puberula, intus fere glabra, staminibus didynamis, antherarum thecis reflexis, ovario oblongo, dense lepidoto; capsula anguste oblonga, subtetragona, alis octo longitudinalibus.

Vine; branchlets terete, glabrous or subpuberulous, when older with scattered, pale, round lenticels, the interpetiolar glandular fields divided, the two halves separated by a nonglandular medial strip; pseudostipules lacking. Leaves 3-foliolate or 2-foliolate with a (presumably simple) tendril or tendril scar, never simple even at the base of branchlets; leaflets ovate to elliptic, acuminate, the base rounded, 3–8 cm long, 1.2–4 cm wide, chartaceous, the main veins plane or prominulous above, slightly raised below, somewhat puberulous along the midvein above, sparsely puberulous or pilose along the main veins below and sometimes scattered subpuberulous on the lower surface, the margins noticeably ciliate, drying brownish olive; petiolules 0.3–1.6 cm long; petioles 1.3–3.5 cm long, varyingly puberulous. Inflorescence a terminal panicle, lepidote and puberulous, bracts and bracteoles linear, to 2 mm long. Flowers with the calyx cupular, puberulous, ca. 2 mm long (with teeth), 2–3 mm wide, 5-denticulate, the teeth 0.5 mm long, extended as ribs on the outside of the calyx; corolla magenta, tubular-infundibuliform, 2.6–3 cm long, 0.9–1.3 cm wide at the mouth

of the tube, the tube 1.8–2 cm long, the lobes ca. 0.5 cm long, puberulous outside and on the lobes inside, the tube mostly glabrous inside, slightly glandular pubescent at the level of stamen insertion; stamens didynamous, inserted 5–6 mm above the base of the corolla, the anther thecae divaricate, pilose, reflexed forward from near the base, ca. 1.5 mm long, the blunt pilose connective extended 0.3–0.4 mm; pistil 1.6–1.7 cm long, the ovary oblong, densely lepidote, 1.5 mm long, 1 mm wide; disc small, pulvinate, 0.3 mm long, 1 mm wide. Capsule linear-oblong, basically subtetragonal, 4–30 cm long, 1.3–2.3 cm wide including the 8 thin longitudinal wings, each wing 3–8 mm wide, glabrous, drying dark brown; seeds thin, bialate, ca. 1 cm long, ca. 3 cm wide, the wings brownish-hyaline, not sharply demarcated from the seed body.

TYPE: BRAZIL. Without locality, *Nadeaud s.n.* (P, holotype; MO, P, isotypes).

Additional collections examined: BRAZIL. RIO DE JANEIRO: Rio Parahyba, 29 Nov. 1880, *Netto et al. s.n.* (R-23675, MO). Baixada Fluminense, Pilar, 30 Dec. 1939, *Lutz 1565* (R-127371, MO). Without locality, *Glaziou 3769* (F). SÃO PAULO: Without locality, *Weir 516* (BM, mixed with flowering material of *Arrabidaea florida* DC.).

This overlooked species is closely related to *C. convoluta* (Vell.) A. Gentry [*C. pterocarpa* (Cham.) DC.] and Sandwith (in herb.) has identified flowering material (*Lutz 1565*) with that species, which differs most conspicuously in a merely 4-winged fruit and a larger much more deeply divided calyx with teeth 2.5–4 mm long. Vegetatively the two are extremely similar but *C. octoptera* differs in having uniformly 2-parted interpetiolar glandular fields (these may be 2-parted, undivided, or absent in *C. convoluta*), typically darker-drying leaves with noticeably ciliate leaflet margins (the leaflet margins of *C. convoluta* are pubescent only in var. *pubescens* Mello which has the whole leaf undersurface pilose), and in the complete absence of simple leaves at the base of vegetative shoots. *Cuspidaria convoluta* ranges from northern Argentina and adjacent Paraguay north to the states of Minas Gerais and Rio de Janeiro in Brazil where it overlaps with *C. octoptera*. However, the two species are probably ecologically separated since all altitudinal records for *C. convoluta* are from above 500 m while *C. octoptera* is apparently restricted to the coastal lowlands.

Lundia virginalis DC. var. **nitidula** (DC.) A. Gentry, comb. nov.

L. nitidula DC., Prodr. 9: 181. 1845. SYNTYPES: Brazil, Minas Gerais, *Martius s.n.* (M, fragment G-DC). Brazil, Sebastianapolitana, *Martius s.n.* (M).
Bignonia nitidula Mart. ex DC., Prodr. 9: 181. 1845, nom. nud., pro syn.

De Candolle (1845) was the first to systematically treat *Lundia*. His specific concepts have proven overly narrow and four of his nine species are now generally regarded as conspecific. Bureau (1868) united *L. hebantha* DC. with *L. virginalis* DC. but maintained *L. nitidula* as specifically distinct. Baillon (1888) was the first to unite these two concurrently published species of de Candolle which differ only in calyx length. Since Baillon adopted *L. virginalis*, that name takes precedence for the species. Later Bureau & Schumann (1896–1897) likewise concluded that *L. virginalis* and *L. nitidula* were conspecific but

chose to unite them under *L. nitidula*, treating the short-calyxed form as *L. nitudula* var. *virginalis* (DC.) Bureau & K. Schum. Since the name for the combined taxon must be *L. virginalis* under Article 57 of the *International Code of Botanical Nomenclature*, the new combination proposed above is needed if the long-calyxed plant is to be recognized at varietal rank. An additional problem in this complex is posed by the existence of a second short-calyxed form which differs in more greenish-drying calyx and leaves, shorter, broader corolla, and white (not magenta) flower color. This has been separated as *L. glazioviana* Kränzl. but was considered a variant of *L. virginalis* by Bureau and Schumann and Sandwith (in herb.).

Memora imperatoris-maximilianii (Wawra) A. Gentry, comb. nov.

Bignonia imperatoris-maximiliani Wawra, Bot. Ergeb. Reise Maximilian Bras. 73, *tab. 10.* 1866. TYPE: Brazil, Bahia, *Wawra & Maly 156* (W).

Pleonotoma imperatoris-maximiliani (Wawra) Bureau & K. Schum. in Mart., Fl. Bras. 8(2): 279. 1897.

In reviewing this species, then known only from the fragmentary type and Wawra's illustration, Sandwith (1959) noted its probable affinity with *Memora* rather than *Pleonotoma* but refrained from proposing the necessary combination. Salient characters of the plant include the 5-denticulate calyx, open paniculate inflorescence, red corolla with both tube and lobes glabrous outside, plate-shaped glands at base of the lobes, triternate leaves with rather large leaflets, and especially the terete branchlets. The latter two characters alone almost mandate placement in *Memora*; all other features are also consistent with this placement.

Memora imperatoris-maximilianii is unusual in *Memora* because of its red flowers but *M. magnifica* (Mart. ex DC.) Bureau has bright orange or red orange flowers and several *Memora* species have yellow orange flowers. The combination of conspicuously 5-denticulate but otherwise truncate calyces and very minutely bracteate inflorescences are matched in *Memora* only by *M. campicola* Pilger which has a very different inflorescence, yellow flowers, and multiple compound leaves with small pubescent leaflets and *M. biternata* A. Samp. which has sessile leaflets and corolla lobes pubescent outside. Both of these species have the thick-foliaceous pseudostipules characteristic of most *Memora* species.

A recent collection apparently attributable to *M. imperatoris-maximilianii* is now available. This is *A. Lima 57-2799* (IAN) from Nazaré da Mata, Pernambuco, and permits amplification of Wawra's description. The most noteworthy additional characteristic is the presence of conspicuous subulate pseudostipules 3–5 mm long (cf. *M. cristicalyx* below). The leaflets of this collection are entire to serrulate and it has the distinctly paniculate inflorescence figured by Wawra. Field notes on the Lima collection describe the flowers as "róseo nos lobos (variando de róseo a lilaz bem claro) e amarelo no tubo; cálice esverd."

Memora cristicalyx A. Gentry, sp. nov.

Memora acutiloba Bureau, Bull. Soc. Bot. France, Mem. 58 (3f): 523. 1911, nom. nud.

Habitus ignotus; ramuli teretes, glabri, sine consociebus glandularum in nodis inter petioles; folia biternata, foliolis anguste ovatis, plerumque serratis; inflorescentia anguste paniculata,

axillaris, plus minusve glabrata; flores calyce campanulato, 5-denticulato dentibus extensis in cristis, glabro, corolla tubulo-infundibuliformi, tubo extus glabro, lobis puberulis, ovario cylindrico dense lepidoto; fructus ignotus.

Habit unknown; branchlets terete, finely striate, glabrous, drying dark with numerous round whitish lenticels, the nodes without interpetiolar glandular fields, with a raised ridge connecting opposite petioles; pseudostipules prominent, linear-subulate, 4–10 mm long. Leaves biternate, the tendril tip not seen; leaflets narrowly ovate, acute to acuminate, basally rounded, usually conspicuously serrate, chartaceous, 2.5–9 cm long, 1.3–4.2 cm wide, mostly glabrate, inconspicuously scattered-lepidote, minutely subpuberulous at the base of the midvein above and below, drying blackish above, dark olive with reddish black midvein below; petiole and petiolules adaxially grooved, subpuberulous. Inflorescence a racemose axillary panicle, the lateral branches subsessile to 1.5 cm long, glabrate to subpuberulous, terminated by a pair of several mm long thinly subulate bracts, these subtending a cluster of 1 to 8 flowers on ebracteolate pedicels up to 2.5 cm long. Flowers with the calyx campanulate, subtruncate, 5-denticulate, the 0.5 mm long teeth extended as raised lateral ridges to the base of the calyx, 6–7 mm long, 5–6 mm wide, glabrous; corolla probably yellow (drying blackish yellow in type), tubular-infundibuliform, ca. 3 cm long, ca. 1 cm wide at the mouth of the tube, the tube ca. 2.5 cm long, the lobes ca. 1 cm long, the tube glabrous and the lobes puberulous outside, the lobes puberulous inside, the tube glabrous inside except at the level of stamen insertion; stamens didynamous, the filaments ca. 1.5 cm long, the anther thecae 3 mm long, somewhat divergent; ovary cylindric, 2 mm long, 1 mm wide, densely minutely lepidote; disc annular-pulvinate, 0.6 mm long, 1.5 mm wide. Fruit unknown.

TYPE: BRAZIL. CEARÁ: Without data, *Fr. Allemão & M. de Cysneiros 1045* (R-127332, holotype; MO, isotype).

Additional collection examined: BRAZIL. Without data, *Glaziou 11232* (P, 2 sheets).

This species is related to *M. imperatoris-maximilianii* (see above) but is otherwise remarkably isolated. Biternate leaves and terete stem mandate placement in *Memora* where it is the only species with serrate leaflets. Ridged calyces, rather reminiscent of *Clytostoma pterocalyx* Sprague, are unique in *Memora* and similar long subulate pseudostipules are found only in *M. imperatoris-maximilianii. Memora imperatoris-maximilianii* differs in an unridged glandular calyx, the corolla lobes glabrous outside and with plate-shaped glands at their bases, entire to subentire leaflets and a more open inflorescence. It is possible that additional collections from poorly known and apparently Bignoniaceae-rich northeastern Brazil will show that this and *M. imperatoris-maximilianii* represent opposite extremes of a variable population but the available evidence suggests specific separation.

The Paris specimens have been annotated by Bureau as "*Memora acutiloba* Bur., n. sp." and that nomen nudum was used in Glaziou's "Liste des plantes du Brésil central recueillies en 1861–1895." I prefer the more descriptive epithet "cristicalyx."

Tabebuia catarinensis A. Gentry, sp. nov.

Frutex ad 3 m altus; folia palmatim (6–)7-foliolata, foliolis oblongo-ellipticis vel obovatis, serratis, glabrescentibus; inflorescentia paniculata, aliquantum congesta, ramis dense stellato-rufescentibus; flores calyce tubulo-campanulato, piloso, corolla lutea, extus glabra, intus fauce puberula, ovario ovoideo, dense lepidoto; capsula anguste oblonga, tomentosa trichomatibus barbatis, irreguliter rugulosa.

Shrub 0.5–3 m tall; twigs terete, striate, minutely and glabrescently stellate-tomentose. Leaves palmately (6–)7-foliolate; leaflets oblong-elliptic to obovate, acute or very briefly acuminate, the base rounded, conspicuously and evenly serrate, the terminal leaflet to 11 cm long and 5 cm wide, the lateral leaflets progressively smaller, chartaceous, when young sparsely stellate-pubescent along the main veins above and below, almost completely glabrescent at maturity, drying blackish or dark olive above and below; petiolules to 4 cm long; petioles 5–13 cm long, glabrescently stellate-tomentose. Inflorescence a several- to many-flowered, short terminal panicle, its branches densely rufescent with stellate, barbate and simple trichomes to 1 mm long, the bracts minute, subulate, to 3 mm long. Flowers with the calyx tubular-campanulate, irregularly 3–5-lobed, 12–20 mm long, 8–12 mm wide, pilose with reddish mostly barbate trichomes to 1 mm long; corolla yellow, tubular-infundibuliform, 5–7 cm long, 1.4–2.2 cm wide at the mouth of the tube, the tube 3.5–5 cm long, the lobes 1–2 cm long, drying dark brown with blackish venation, glabrous, the tube glabrous outside, inside pubescent with rather short (0.5–0.8 mm long) stiff erect trichomes descending from sinuses of the corolla lobes to above the level of stamen insertion, more or less glabrous at and below stamen insertion; stamens didynamous, inserted ca. 10 mm above the base of the corolla tube, the filaments 1.7–2.2 cm long, the staminode ca. 6 mm long, the anther thecae widely divergent, 3 mm long; pistil 3.2–3.4 cm long, the ovary ovoid, ca. 2 mm long, 1.3–1.5 mm wide, densely lepidote, drying blackish, the ovules ca. 4-seriate in each locule; disc shortly cylindric, 1 mm long, 2 mm wide. Capsule linear-oblong, 5–9 cm long, 1.5–1.8 cm wide, densely reddish-brown tomentose with mostly barbate trichomes ca. 0.5 mm long, the surface finely and irregularly rugulose, not regularly striate; seeds (very immature) bialate, the wings hyaline membranaceous.

TYPE: BRAZIL. SANTA CATARINA: Monte Crista, Garuva, campo, 750 m, arbusto 2 m, flores amarela, 21 Oct. 1966, *Klein & Ravenna 6834* (K).

Additional collections examined: BRAZIL. SANTA CATARINA: Monte Crista, Garuva, 750 m, campo, arbusto 2 m, fruto imaturo marron, 21 Oct. 1966, *Klein & Ravenna 6828* (K); matinha, flor amarela, arbusto 3 m, 21 Oct. 1966, *Klein & Ravenna 6843* (K); 900 m, campo, arbusto 0–5 m, flores amarela, 2 Sep. 1960, *Reitz & Klein 9790* (K). Morro do Campo Alegre, São Francisco do Sul, 1,200 m, campo, arbusto 1 m, flores amarela, 3 Sep. 1960, *Reitz & Klein 9766* (K); sterile, 24 Mar. 1961, *Reitz & Klein s.n.* (K). PARANÁ: Mun. Campina Grande do Sul, Pico Caratuva, 1,950 m, arbusto do topo do morro, flor amarela, 5 Oct. 1967, *Hatschbach 17325* (MO).

This species is superficially most similar to *T. bureauvii* Sandw. endemic to the vicinity of Rio de Janeiro. That species differs in being a tree to 12 m tall and in having a very shortly stellate-rufescent calyx with black-drying plate-shaped glands, a fewer-flowered, more finely tomentose inflorescence, a sparsely papillose-puberulous corolla throat, a longer (ca. 4 mm long) ovary, narrower

leaflets, and longer, smooth-surfaced glabrous fruit. The new species was supposed by Sandwith & Hunt (1974) to be a form of *T. chrysotricha* (Mart. ex DC.) Standley. A hybrid origin from that species and *T. alba* (Cham.) Sandw. was also suggested as the new species is intermediate in most respects between these two species, both of which occur in Santa Catarina. *Tabebuia catarinensis* is ecologically distinct from lowland *T. chrysotricha* (below 800 m) but not from *T. alba.* Its flowers and inflorescence are identical to those of *T. alba* of which it could be a glabrescent-leaved derivative. However, the shrubby habit, shorter rough-surfaced (not striate) fruit, and uniformity of the strikingly different glabrate, rather than densely canescent, leaves support specific recognition. Hatschbach (personal communication) reports that the new species can be rather common locally at high altitudes in the Serra do Mar.

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NEW RECORDS OF APOCYNACEAE FOR PANAMA AND THE CHOCO[1]

Alwyn H. Gentry[2]

Abstract

Tabernaemontana pendula and *T. longipes*, synonymized under *T. chrysocarpa* in the *Flora of Panama*, are recognized as distinct from it. *Stemmadenia allenii* was originally described from fruiting and flowering material of different species, one of which—the most common wet-forest species of the genus in Panama—is now described as *S. minima* A. Gentry. The first South American record of the North American *Tabernaemontana arborea*, the first North American record of the South American *Odontadenia cognata*, and the reconfirmation of the occurrence of *Fosteronia myriantha* in Panama are reported.

Panamanian plants referred to *Tabernaemontana chrysocarpa* in the *Flora of Panama* treatment (Nowicke, 1970) prove to represent three distinct species. These three species, somewhat similar on the basis of floral characteristics, are easily separated by vegetative and fruiting characters.

Tabernaemontana pendula Woodson

This species was described from a single specimen from El Valle (*Allen 1734*). It was compared by Woodson (1940) with *T. amygdalifolia* Jacq. because of its exserted anthers but lumped with *T. chrysocarpa*, a species characterized by included or subexserted anthers, by Nowicke (1970) in the *Flora of Panama*. *Tabernaemontana pendula* has a much longer peduncle than either *T. amygdalifolia* or *T. chrysocarpa*. It also has wider, more elliptical leaves and a characteristically wrinkled-reticulate fruit surface. The long peduncle is also obvious in fruit. The fruit, previously undescribed, is similar in shape to that of *T. chrysocarpa*. Two additional collections of this species, both in fruit, are now at hand. These are *Mori et al. 1912* from La Mesa (above El Valle), Coclé Province, and *Mori & Kallunki 2028* from the Río Guanche area of Colón Province.

Tabernaemontana longipes Donnell Smith

This species was described from Costa Rica and has been thought endemic to that country. It is closely related to *T. chrysocarpa* and the Panamanian specimens of *T. longipes* were included with that species in the *Flora of Panama*. Vegetatively *T. longipes* differs from *T. chrysocarpa* in its elliptic leaves, always broadest near the middle; the latter has narrowly obovate to oblanceolate-elliptic leaves, broadest above the middle. The fruit of *T. longipes*, previously undescribed, is very distinctive with a verrucose muricate-ridged surface quite unlike the smooth, papillose or finely reticulate-ridged fruits of other Panamanian species of *Tabernaemontana* and *Stemmadenia*. I have seen no fruits of this

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species from Costa Rica, but the Costa Rican and Panamanian collections seem indistinguishable on the basis of vegetative and floral characters.

Tabernaemontana longipes has been collected in Panama only above El Valle de Antón, Coclé Province, where it is locally very common. It is represented by thirteen collections from El Valle in the Missouri Botanical Garden Herbarium including all the Coclé Province collections cited as *T. chrysocarpa* in the *Flora of Panama* except *Allen 1734* which is *T. pendula* (see above). The additional collections of this species—*Kennedy et al. 3035*, *Liesner 747*, *Croat 14383*, *Gentry & Dwyer 3612*, and *Gentry 6873*—were all identified and distributed as *T. chrysocarpa.*

The four Panamanian *Tabernaemontana* species with anthers tinged blue green can be separated by the following key:

a. Anthers exserted or half-exserted; follicles narrow (more than twice as long as wide) or reniform and finely reticulate-wrinkled.
  b. Peduncle very long, exceeding the leaves; fruit reniform and finely reticulate .... *T. pendula*
  bb. Peduncle not elongate, inflorescence not exceeding the leaves; fruit narrowly elliptic, smooth .... *T. amygdalifolia*
aa. Anthers included or barely exserted; follicles reniform, smooth or verrucose and muricate-ridged.
  c. Leaves narrowly obovate to oblanceolate-elliptic, broadest above the middle; fruit smooth .... *T. chrysocarpa*
  cc. Leaves elliptic, broadest at the middle; fruit verrucose and muricate-ridged .... *T. longipes*

Tabernaemontana arborea Rose

This species has previously been recorded from Belize to Panama. It is easily recognized by its yellow anthers inserted near the base of the corolla tube. Like many other "Central American" species, it also occurs in the northern Chocó. Two Chocó collections have been seen—*Duke 12233* (MO, NY, OSU) and *Duke 11169* (OSU), both from the Río Truando.

Stemmadenia allenii Woodson

This species, described from El Valle, Panama, was separated by Woodson from closely related Costa Rican *S. alfari* (Donnell Smith) Woodson because of its longer calyx lobes and larger corolla with broader throat and longer lobes. The type collection of *S. allenii* is in fruit and the fruit is of the same narrow, long-acuminate form as that of *S. alfari.* Many fruiting collections of *S. allenii* are now at hand, all with fruits of the same characteristic slender form. However, a vegetatively similar species with a very different obovoid to almost orbicular fruit also occurs in the same wet-forest areas and the flowering material attributed to *S. allenii* by Woodson (1941) and Nowicke (1970) actually belongs to the thick-fruited species (see below). The first flowering collection of the real *S. allenii* is *Liesner 765* (MO) from El Valle, the type locality, which has the corolla throat narrower (rather than broader!) than *S. alfari* and calyx lobes only 4–5 mm long; in fact *S. allenii* proves separable from *S. alfari* not by the characteristics cited by Woodson but by their opposites! The real *S. allenii*

keys out to S. *alfari* in the *Flora of Panama*, but that species does not occur in Panama unless S. *allenii* itself should be considered as merely a geographic variant.

Stemmadenia minima A. Gentry, sp. nov.

Frutex lactifer. Folia parva, anguste elliptica, acuminata, glabra. Flor calycis lobis membranaceis, 4–10 mm longis, corolla infundibuliformi, albida, tubo torto, staminibus tubo corollae prope mediam insertis. Folliculi crassi, obtusi, fere suborbiculati.

Shrub or small tree 1.5–5 m tall; branchlets somewhat angulate, minutely papillose, lactiferous. Leaves small, narrowly elliptic, acuminate, cuneate at the base, to 11 cm long and 3.9 cm wide (largest leaf 1.9–3.9 cm wide, $\bar{x}$ = 2.97 cm), glabrous above and below, membranous; petioles 2–10 mm long, not clearly differentiated from the leaf base. Inflorescence a single flower, terminal from between two dichotomous lateral branches, glabrous, with a minute triangular bracteole; calyx lobes inequal, membranous, narrowly oblong, 4–10 mm long, glabrous; corolla infundibuliform, white to cream, the tube proper 12–17 mm long, twisted 180° at the top, the throat 15–20 mm long, the lobes obovate, ca. 1 cm long; stamens attached at the middle of the corolla tube, the anthers 4–5 mm long. Follicles thick, blunt, almost orbicular ("obovoid subreniform"), 2–3 cm long, 1.5–2.5 cm broad.

TYPE: PANAMA. PANAMÁ: Cerro Jefe, 800–1,000 m, 21 Dec. 1972, *Gentry 6763* (MO, holotype; duplicates were distributed as S. cf. *alfari*).

Additional collections examined: PANAMA. CANAL ZONE: Madden Lake, *Dwyer & Lallathin 8827A* (MO). COCLÉ: El Valle, *Allen 2239, 2364*; *Croat 25347*; *Dwyer et al. 4502a* (all MO). COLÓN: Santa Rita Ridge, *Gentry 6090, 6562* (both MO). PANAMÁ: Cerro Campana, *Busey 861*; *Croat 12144*; *Dressler 3523*; *Dwyer & Kirkbride 7829A*; *Gentry 4934*; *Mori & Kallunki 1930*; *Porter et al. 5249* (all MO). Cerro Jefe, *Croat 13028, 14444*; *Dressler 3333*; *Duke 9449* (all MO). El Llano-Cartí Road, *Gentry 5071*; *Gentry et al. 14201, 14214*; *Mori & Kallunki 2915* (all MO). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2853* (MO).

This species has been generally confounded with S. *allenii*, and, in fact, the original description of the flowers of that species are based on S. *minima* (see above). Discovery of the short thick fruits of S. *minima* prove that it is quite unrelated to S. *allenii* which has narrow, long-acuminate fruits. Calyx lobe length of these plants also exceeds that of S. *allenii* and, in fact, approaches that of S. *lagunae* Woodson, otherwise reported only from Bocas del Toro Province. I have previously identified collections of this entity as S. *lagunae*, which has a similar thick, rounded fruit. Numerous additional collections of S. *minima* are now at hand and it proves to differ constantly from S. *lagunae* in smaller leaves [largest leaf 1.9–3.9 cm wide ($\bar{x}$ = 2.97 cm) versus largest leaf 4.3–6.2 cm wide ($\bar{x}$ = 5.32 cm)] as well as shorter ($\bar{x}$ for longest lobe = 8.05 mm versus 17.2 mm), narrower, not at all imbricate calyx lobes. It usually has white flowers (sometimes pale yellow or white with a yellowish center) while S. *lagunae* has yellow flowers (one collection reported as light yellow) and has a distinct geographic distribution. No collections are available from the critical area between Santa Fé de Veraguas where S. *lagunae* occurs and El Valle, the westernmost locality for S. *minima*, but the available evidence suggests specific recognition.

Stemmadenia minima is fairly common in all the accessible middle elevation wet-forest areas of eastern and central Panama and is the only wet-forest species of *Stemmadenia* occurring east of the Canal Zone. It overlaps with *S. allenii* at El Valle and Cerro Campana but can be easily distinguished from that species by its very different fruit, wider corolla throat, smaller, less membranous leaves, longer calyx lobes and paler flower color.

Forsteronia myriantha Donnell Smith

This species was not treated in the *Flora of Panama* although Woodson (1935) had reported it from the Republic on the basis of a single Hayes collection. It has recently been recollected in Panama (*Foster 4107*, Barro Colorado Island, Canal Zone). The two Panamanian collections key to this species but have the petals sparsely pilosulose both inside and outside. Although this disagrees with Woodson's description of the petals as glabrous or very minutely papillate without, the type (*Heyde & Lux 4533* from Guatemala) also has a few long trichomes on the outside of some petals and otherwise matches the Panamanian material. *Forsteronia myriantha* differs vegetatively from the other Panamanian species in having long trichomes scattered along the leaf midvein and sometimes over the surface beneath as well as in the nerve axils.

Odontadenia cognata (Stadelm.) Woodson

This widespread South American species was cited from extreme eastern Panama by Woodson (1935) based on a single immature collection from Puerto Obaldia, but was subsequently rejected from the *Flora of Panama.* Ten Panamanian collections are now at hand, all collected in wet-forest areas during the last few years. It is the most common species of *Odontadenia* on the El Llano-Cartí road and has also been collected on Santa Rita Ridge, Colón Province, and above Santa Fé, Veraguas Province. The species also reaches Costa Rica, based on *Opler 1724* (MO) from La Selva, Heredia Province. *Odontadenia cognata* is easily told from *O. puncticulosa*, which it somewhat resembles, by the corolla tube tapering more evenly to a narrower base with the anthers inserted near the base of the tube proper rather than at the base of the throat. Several collections are noted as having pink or orange red corollas, but I have seen corollas of the more frequently reported yellow or pale yellow color only. Similar color variations occur in South America but do not appear taxonomically significant.

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NEW TAXA AND COMBINATIONS IN *ERAGROSTIS* (POACEAE)[1]

JOHN T. WITHERSPOON[2]

ABSTRACT

Eragrostis guatemalensis Witherspoon and *E. intermedia* Hitchc. var. *appressa* Witherspoon are described as new. The former is distinguished from other North American *Eragrostis* by having long pilose hairs on the lemmas and paleas. The latter is distinguished from other members of the *E. intermedia* group by its short lemmas and appressed primary branchlets and pedicels. In addition, four new combinations are made—*E. intermedia* var. *oreophila* (L. H. Harvey) Witherspoon, *E. intermedia* var. *praetermissa* (L. H. Harvey) Witherspoon, *E. hirta* Fourn. var. *longiramea* (Swallen) Witherspoon, *E. trichocolea* Hack. & Arech. var. *floridana* (Hitchc.) Witherspoon—and keys are provided to the varieties of *E. intermedia*, *E. hirta*, and *E. trichocolea*.

Eragrostis guatemalensis Witherspoon, sp. nov.

Species *E. intermediae* varietatum *intermediae* et *praetermissae* affinis, sed differt ab utroque paucis pilosis propre margines lemmatum et palearum et a prima innovationibus extravaginalis, a secunda paniculis axillis dense pilosis, nervis lateralibus inconspicuis, et caryopsibus valde sulcatus.

Perennial, 65–115 cm tall. *Culms* erect to ascending from a somewhat knotty base, sometimes geniculate at the middle nodes; innovations extravaginal, infrequently intravaginal, few to many, variously papillose-pilose. *Leaves* 4–8 per culm; sheaths slightly overlapping below, shorter than the internodes above, sparsely to densely papillose-pilose over the rounded back, along the margins and on the sides of the collar, particularly dense in the region between the margins and the "keel," occasionally glabrate; ligules 0.3–0.4 mm long; blades linear-lanceolate, attenuate, flat to involute, 10–22 cm long, 2–5 mm wide, with dense supraligular hairs and scattered to dense papillose-pilose pubescence on the adaxial surface, glabrous to densely papillose-pilose abaxially. *Panicles* elliptic to ovate, open, 24–30 cm long, 12–21 cm wide, very long exserted when mature; branches 24–30 per panicle, 10–13 cm long, ascending to spreading, curved or flexuous, floriferous 0.8–2.5 cm above the base, the lower ones solitary, paired or in verticels, the upper likewise and equidistant, the primary axils pilose laterally and adaxially, occasionally bearded all around the branch bases, the secondary axils often pilose laterally; primary branchlets 4–10 per branch, 30–46 mm long, ascending to spreading, capillary, mostly flexuous; secondary branchlets 0–2 per primary branchlet, mostly ascending, capillary, flexuous; pedicels 5–10 mm long ascending to spreading, capillary, flexuous. *Spikelets* 2–8 per primary branchlet, oblong to ovate, acute, slightly compressed, dark green to plumbeous or brownish, 3–8-flowered, 3.5–7 mm long, 1.2–2.1 mm

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wide, the florets slightly imbricate; glumes with hyaline margins and membranous bodies or the first hyaline throughout, scabrous on the keels, the first ovate-lanceolate, acuminate, 1–1.5 mm long, 0.5–0.7 mm wide, the second ovate, acute, 1.5–2 mm long, 1–1.2 mm wide; lemmas ovate, acute, rounded on the back below, scabrous on the keel above, the margins and tips hyaline, the bodies membranous, often tinged with reddish purple, 2–2.4 mm long, 1.2–1.5 mm wide, the lateral nerves inconspicuous, 2–6 pilose hairs ca. 0.5 mm long in a longitudinal row on the broadest part of the lemmas between the lateral nerves and the margins, the hairs fragile and caducous; paleas with hyaline margins and membranous bodies, usually also hyaline between the keels on the evenly convex back, ciliolate on the keels, 1.4–1.8 mm long, often with a row of hairs similar to those on the lemmas, the hairs in a longitudinal row between the keels and the margins. *Caryopses* oblong, strongly grooved adaxially, 0.6–0.8 mm long, 0.4–0.5 mm wide, 0.4–0.5 mm thick.

TYPE: GUATEMALA: Alamedo, 15 July 1937, *J. R. Johnston 930* (F, holotype).

Paratypes: GUATEMALA: Solola, San Pedro, *Steyermark 47100* (F, US). Guatemala, *Aguilar 345* (F).
MEXICO. MEXICO, between Nicolás Romero and Progreso Industrial, *Sohns 540* (US). 4 mi E of Ixtlhuaca, *Soderstrom 515* (US). PUEBLA: El Chamizal, mun. de Mazapiltepec, *Ventura A. 1729* (ENCB).

This new species is similar in many respects to *Eragrostis intermedia* Hitchc. var. *intermedia* and *E. intermedia* var. *praetermissa* (proposed below). It differs from the first by the hairs on the lemmas and paleas and by the pubescence on the foliage. It differs from the second by the hairs on the lemmas and paleas and by the inconspicuous lateral nerves.

The only other known species of the *E. intermedia* group in the Western Hemisphere with hairs on the body of the lemma is the South American *E. seminuda* Trin. However, the latter is a strikingly different taxon with extremely long, villous, involute blades and a very large, diffuse panicle. The spikelets of *E. seminuda* are smaller and have only three or four florets. The relationships of *E. seminuda* seem to lie more with *E. polytricha* Nees and *E. trichocolea* Hack. & Arech. s. lat.

Eragrostis guatemalensis occurs between 1,900 and 2,650 m on rocky mountain slopes and in oak-pine forests of central Mexico and central Guatemala. The specific epithet was derived from the taxon's occurrence in Guatemala. When first discovered among specimens from the Field Museum (F), the only known collections were those from Guatemala. Since then, however, it has been found from the states of Mexico and Puebla in Mexico.

Eragrostis intermedia Hitchc. var. **appressa** Witherspoon, var. nov.

Varietas oreophilae affinis, sed differt lemmatibus brevioribus et pedicellis appressis.

Perennial, 31–63 cm tall. *Culms* erect, weakly tufted, strongly anthocyanic; innovations intravaginal, rarely extravaginal, few, glabrous. *Leaves* 2–4 per

culm; sheaths overlapping below, slightly exceeding to slightly shorter than the internodes above, pilose along the margins and on the collar sides and throat; ligules 0.2–0.3 mm long; blades linear-lanceolate, acuminate-attenuate, flat or involute below, tightly involute above, appressed or ascending, 2–9 cm long, 1–2 mm wide, densely pilose above the ligule and a short way up the adaxial surface. *Panicles* elliptic when young, mostly deltoid when mature, open to somewhat condensed, stiff, straight or curved at the tip, 12–24 cm long, 5–20 cm wide, short to long exserted; branches 10–24 per panicle, 5–13 cm long, appressed-ascending to ascending-spreading, infrequently spreading, straight, floriferous 0.9–3.1 cm above the base, the primary and secondary axils pilose laterally and abaxially, occasionally also adaxially; primary branchlets 0–9 per branch, 13–45 mm long, appressed to ascending, capillary; secondary branchlets absent; pedicels 1–6 mm long, appressed to appressed-ascending, capillary. *Spikelets* 1–6 per primary branchlet, ovate, acute, barely compressed, reddish purple, 3–5-flowered, 2.4–3.7 mm long, 1.2–1.6 mm wide, the florets slightly imbricate, tightly so when young; glumes hyaline or the second with hyaline margins and a membranous body, strongly scabrous on the keels, the first lanceolate to ovate, acuminate to acute, 1–1.5 mm long, 0.5–0.6 mm wide, the second ovate, acute, 1.3–1.6 mm long, 0.7–0.8 mm wide; lemmas ovate to broadly so, acute, rounded or slightly keeled below, scabrous on the keel above, the tips hyaline, the bodies membranous, often tinged with reddish purple, 1.5–1.7 mm long, 1–1.4 mm wide, the lateral nerves very weak; paleas hyaline, ciliolate on the keels, 1.2–1.5 mm long. *Caryopses* oblong to quadrate, weakly grooved adaxially, reticulate, 0.5–0.7 mm long, 0.3–0.5 mm wide, 0.3–0.5 mm thick.

TYPE: MEXICO. JALISCO: 7 mi S of Zacatecas-Jalisco border, 11 Oct. 1972, *Harvey & Witherspoon 9344* (US, holotype; ENCB, MO, MONTU, NY, RM, TAES, W, isotypes).

This taxon is phenetically close to *Eragrostis intermedia* var. *oreophila* (proposed below) but is distinguished from it by its shorter lemmas and appressed pedicels.

This variety is known only from the type locality. The area is a roadside swale containing limestone, at approximately 1,830 m. The vegetation is sparse and the plants of var. *appressa* grow in small tufts scattered throughout the area. Oaks and junipers are common on the margins of the swale.

The plants are a striking deep-red color and upon emergence from the sheath, the panicles appear spikelike, resembling a *Sporobolus* or *Muhlenbergia* with narrow, compact panicles. All orders of branching remain appressed for some time following emergence, but even after the main branches spread, the primary branchlets and pedicels remain appressed, hence the derivation of the name.

Eragrostis intermedia Hitchc. var. **oreophila** (L. H. Harvey) Witherspoon, comb. et stat. nov.

Eragrostis oreophila L. H. Harvey, Bull. Torrey Bot. Club 81: 407. 1954. TYPE: Mexico, Hidalgo, Jacala, stony mountain side, 4,500 ft, 29 June 1939, *V. H. Chase 7223½* (US, holotype; ARIZ, GH, MICH, MO, TEX, isotypes).

This variety occurs primarily on mountain slopes in central Mexico. It grows in fairly deep, sandy-clay soils at elevations above 1,380 m.

It is not a common taxon in most of its range, but seems to be quite abundant in the mountains around Jacala, Hidalgo. It is known from single collections in both Baja California and Nuevo León. The wide separation of these collections may reflect inadequate sampling but it may be an indication that the taxon has arisen more than once. Variety *intermedia* is common in all these areas. However, the two taxa remain relatively distinct in these areas of sympatry. One collection from Chihuahua (*Gentry 8157*, Sierra Charuco, MICH, UC, US) has pubescent foliage not characteristic of other known specimens.

Eragrostis intermedia Hitchc. var. **praetermissa** (L. H. Harvey) Witherspoon, comb. et stat. nov.

Eragrostis praetermissa L. H. Harvey, Bull. Torrey Bot. Club 81: 408. 1954. TYPE: Guatemala, Dept. Baja Verapaz, Santa Rosa, July 1887, *H. von Türckheim 1292* (US, holotype).

Eragrostis intermedia var. *praetermissa* occurs at high elevations in Mexico and Central America. It grows primarily in the pine-oak zone in deep, loamy soils.

It is not common in any part of its range but may be more prevalent than herbarium material indicates. Since it grows in seemingly native vegetation, most collectors would probably not encounter it if they botanize mostly along roads and established trails.

This variety, although more common than var. *oreophila*, is perhaps not as distinct. Intermediates between var. *intermedia* and var. *praetermissa* have been noted rarely, but var. *praetermissa* can usually be distinguished by its extravaginal buds and papillose-pilose sheaths.

The following key will effectively separate the varieties of *Eragrostis intermedia*.

a. Buds extravaginal; at least the lower sheaths densely papillose-pilose; blades usually flat, often exceeding 5 mm wide; spikelets dark green, the lemmas with strong lateral nerves, rarely weak .... var. *praetermissa*

aa. Buds mostly intravaginal; sheaths glabrous except for a tuft of hairs at the apex or with scattered hairs; blades mostly involute, usually less than 5 mm wide; spikelets light green to plumbeous, often reddish, the lemmas with weak to inconspicuous lateral nerves, rarely strong.

b. Panicles decompound, with secondary branchlets at least on the lower primary branchlets, averaging more than 6 primary branchlets per branch; leaves few to many, not crowded at the base; pedicels generally equal to or shorter than the spikelets .... var. *intermedia*

bb. Panicles lacking secondary branchlets, usually with less than 4 primary branchlets per branch; leaves few, crowded at the base; pedicels generally longer than the spikelets.

c. Branchlets and pedicels appressed to the main branches; lemmas less than 1.8 mm long .... var. *appressa*

cc. Branchlets and pedicels ascending to spreading; lemmas greater than or equal to 1.8 mm long .... var. *oreophila*

Eragrostis hirta Fourn. var. **longiramea** (Swallen) Witherspoon, comb. et stat. nov.

Eragrostis longiramea Swallen, J. Wash. Acad. Sci. 21: 437. 1931. TYPE: Mexico, Tamaulipas Sierra de San Carlos, Pico del Diablo, vic. Marmolejo, 12 Aug. 1930, *H. H. Bartlett 10910* (US, holotype; GH, LHH,[3] MICH, isotypes).

This variety occurs in dry, rocky soils along forest borders and streams from 900 to 3,500 m. Its distribution is generally more northern than typical var. *hirta*. It is known only from the mountains of Tamaulipas, Nuevo León, and San Luis Potosí in Mexico.

Variety *longiramea* is much larger than var. *hirta*, often approaching 2 m in height. The two varieties are quite similar vegetatively, var. *longiramea* usually having more flattened, longer and wider blades. However, they are easily distinguished by their panicles, as shown in the following key.

a. Panicle less than or equal to 45 cm long and 10 cm wide, the branches less than or equal to 10 cm long .... var. *hirta*
aa. Panicle greater than 50 cm long and 18 cm wide, the branches greater than 15 cm long .... var. *longiramea*

Eragrostis trichocolea Hack. & Arech. var. **floridana** (Hitchc.) Witherspoon, comb. et stat. nov.

Eragrostis floridana Hitchc., Amer. J. Bot. 2: 308. 1915. TYPE: United States, Florida, dry pine woods near Tampa, Oct. 1885, *A. H. Curtis 3494* [US, holotype; BR, F, ISC, LE, M, MO, NY (2), PH, TAES, TENN, US (2), isotypes].

Eragrostis purpusii Jedw., Bot. Arch. 5: 201. 1924. TYPE: Mexico, Puebla, Cerro de Gavilan, Aug. 1909, *C. A. Purpus 4084* (UC, lectotype, here designated; US, fragment of holotype ex B). The holotype was destroyed in Berlin; the US fragment consists only of a small branch with a few spikelets.

Eragrostis trichocolea var. *floridana* is found in sandy pinelands in coastal and central Florida and in sandy ground near Huntsville, Texas. It also occurs in sandy ground and sandy pine forests in central Mexico and Central America at higher elevations.

This variety is distinguished by its smaller lemmas, more pubescent foliage and its distribution.

Hitchcock described *E. floridana* in 1915 based on collections from Florida and Orizaba, Mexico. However, after seeing material of *E. trichocolea* in European herbaria, he decided that *E. floridana* was conspecific with that taxon. From notes on the type specimen of *E. floridana* at US, he apparently made this change in 1918 and the taxon was treated as *E. trichocolea* in both editions of *Manual of the Grasses of the United States* (1935 and 1950). However, Hitchcock had not seen the holotype of *E. trichocolea* that is housed in Montevideo (MVM). The "types" seen by Hitchcock and most other North American workers were fragments of two Arechavaleta collections procured by Agnes Chase in 1922 and placed in the U.S. National Herbarium. She obtained these fragments from the Hackel Herbarium in Vienna and the labels on those specimens do not match the label on the holotype. Therefore, the fragments at US do not represent types, although they are, in fact, *E. trichocolea* var. *trichocolea*.

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[3] LHH denotes the personal herbarium of Dr. L. H. Harvey, University of Montana.

After examining the holotype and other South American material, I feel that the North and Central American specimens are phenetically distinct at the varietal level.

Eragrostis purpusii falls within the morphological limits of *E. trichocolea* var. *floridana.*

The varieties of *Eragrostis trichocolea* may be distinguished by the following key.

a. Lemmas greater than or equal to 1.8 mm long and 1.4 mm wide, averaging over 2 mm in length; blades variously papillose-pilose less than ⅓ their length; South American .... var. *trichocolea*

aa. Lemmas less than or equal to 1.8 mm long and 1.3 mm wide, averaging less than 1.7 mm in length; blades densely papillose-pilose at least ⅔ their length; North and Central American .... var. *floridana*

REALIGNMENT OF THE SPECIES PLACED IN *EXOGONIUM* (CONVOLVULACEAE)[1]

DANIEL F. AUSTIN[2]

Exogonium has never been widely accepted as a genus although there have been proponents of this rank since Choisy (1834, 1838, 1845) first described the taxon. House (1908), Matuda (1963) and Standley & Williams (1970) have been among the recent authors keeping the species as a separate genus. Others have suggested that the species could better be ranked at some infrageneric level. Grisebach (1864) reduced it to a section of *Ipomoea*, while Meisner (1869) considered the plants a subgenus.

Since the origin of the name *Exogonium* by Choisy (1834) 31 species have been placed in the taxon, many authors varying the definition of the group slightly. Although usually unstated, the major criteria for inclusion in the taxon were red flowers, salverform corollas, and exserted stamens and stigmas. Floral morphology suggests that the species included in *Exogonium* are mostly adapted for bird pollination; the species exhibit the characters classically associated with this syndrome (van der Pijl, 1960, 1961; Meeuse, 1961; Percival, 1965; Faegri & van der Pijl, 1971). However, a polyphyletic taxon has been created because species from several lines have been lumped solely on the basis of a common pollination system.

The following treatment is a revision of the binomials placed in *Exogonium*. Several other related species are also included. Some of the nomenclatural and biological problems within *Ipomoea* have been discussed elsewhere (Verdcourt, 1957, 1963; Austin, 1975a, 1975b).

Consideration of all morphological criteria indicates that the species proposed for inclusion in *Exogonium* should be placed in the following taxonomic groups.

Group 1. *Exogonium velutifolium* House [Bull. Torrey Bot. Club 35: 100. 1908. TYPE: Mexico, Oaxaca, *Nelson 1877* (GH, holotype; US, isotype)] is not a member of the Convolvulaceae but the Acanthaceae. The correct name is *Ruellia velutifolia* (House) Wasshausen & Austin (Phytologia 25: 433–437. 1973).

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Specimens in the herbaria at A, FAU, F, G, GH, IJ, K, L, LE, M, MEXU, MO, NY, US, and W were examined during visits and on loan. Except where types are cited from other herbaria, material from these institutions formed the basis of the study. My thanks are extended to curators and staff of the institutions cited. K. R. Robertson (Arnold Arboretum) has revised the genus *Jacquemontia* and provided especially useful comments. W. G. D'Arcy (Missouri Botanical Garden) criticized the original manuscript.

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ANN. MISSOURI BOT. GARD. 64: 330–339. 1977.

Group 2. *Exogonium filiforme* (Desr.) Choisy is the only member of the genus *Jacquemontia* with bird-pollinated flowers. The small seeds and capsule which breaks into several sections at dehiscence, among other characteristics, support the conclusion that this is a *Jacquemontia* (see Robertson, 1971).

Jacquemontia solanifolia (L.) Hall. f., Bot. Jahrb. Syst. 16: 542. 1893.

Basionym: *Ipomoea solanifolia* L., Sp. Pl. 161. 1753. LECTOTYPE: *Ipomoea foliis cordatis* Plumier, Cat. Pl. Amer., p. 3 in Nova Pl. Amer. Gen. *Tab. XCIV. fig. 1.*

Synonyms: *Quamoclit solanifolia* (L.) Choisy in DC., Prodr. 9: 335. 1845. *Exogonium solanifolium* (L.) Britton, Mem. Brooklyn Bot. Gard. 1: 82. 1918.

Ipomoea filiformis Jacq., Enum. Pl. Carib. 13. 1760; Sel. Stirp. Amer. 27, *pl. 19.* 1763. LECTOTYPE: illustration by Jacquin, *pl. 19.* 1763. *Convolvulus filiformis* (Jacq.) Desr. in Lam., Encycl. Méth. Bot. 3: 555. 1789. *Exogonium filiforme* (Jacq.) Choisy, Mem. Soc. Phys. Genève 8: 129. 1838.

Distribution: Puerto Rico, Guadalupe, Antigua, St. Barthelemy, St. Croix, St. Thomas, Martinique, Tortola.

Group 3. House included *Exogonium racemosum, E. wrightii* and *E. rudolphii* in his concept of the genus. These three names have been reduced to two species and placed in *Turbina* by O'Donell (1960) and Liogier (1968). The accrescent sepals indicate that this is the proper disposition. A new combination does need to be made.

1. **Turbina racemosa** (Poir.) D. Austin, comb. nov.

Basionym: *Ipomoea racemosa* Poir. in Lam., Encycl. Méth. Bot. Suppl. 4: 633. 1816, non Roth, 1821, nec Griseb., 1866. TYPE: St. Domingo. Possibly in LAM-P, not in the microfiche. Interpretation based on the protologue.

Synonyms: *Convolvulus racemosus* (Poir.) Sprengel, Syst. Veg. 1: 600. 1825. *Exogonium racemosum* (Poir.) Choisy, Mem. Soc. Phys. Genève 8: 128. 1838.

Calystegia berterii Sprengel ex Hall. f., Bot. Jahrb. Syst. 16: 558. 1893, nom. nud., pro syn.

Ipomoea bracteata Rudol. ex Ledeb. in Schrad., Neues J. Bot. 2: 292. 1807, non Cav., 1799. TYPE: St. Domingo, *Rudolphi* (not at LE). *Ipomoea rudolphii* Roem. & Schult., Syst. Veg. 4: 222. 1819. *Pharbitis bracteata* (Rudol. ex Ledeb.) Choisy in DC., Prodr. 9: 344. 1845. *Rivea bracteata* (Rudol. ex Ledeb.) Hall. f., Bot. Jahrb. Syst. 18: 158. 1894. *Turbina rudolphii* (Roem. & Schult.) O'Donell, Lilloa 30: 64. 1960.

Convolvulus altissimus Sprengel, Syst. Veg. 1: 613. 1825. TYPE: Hispaniola, *Bertero* (MO, isotype). *Ipomoea altissima* (Sprengel) Bert. ex G. Don, Gen. Syst. 4: 273. 1838.

Distribution: Cuba, Haiti, Dominican Republic.

2. *Turbina wrightii* (House) Alain, Brittonia 20: 152. 1968.

Basionym: *Exogonium wrightii* House, Bull. Torrey Bot. Club 35: 99. 1908. TYPE: Cuba, *Wright 1650* (GH, holotype; MO, isotype).

Synonyms: *Ipomoea wrightii* (House) Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22: 123. 1955.

Ipomoea racemosa sensu Griseb., Cat. Pl. Cub. 205. 1866, non Poir., 1816.

Distribution: Endemic to Cuba.

Group 4. Three binomials illustrated by Sessé & Moçiño have been placed in *Ipomoea* sect. *Quamoclit* by Choisy (1845) and O'Donell (1959). Their caudate sepals clearly indicate affinity with that species group.

1. *Ipomoea hastigera* H.B.K., Nov. Gen. Sp. Pl. 3: 87. 1819; O'Donell, Lilloa 29: 42. 1959.

Exogonium curviflorum Sessé & Moçiño ex Choisy in DC., Prodr. 9: 336. 1845, nom. pro syn.

2. *Ipomoea neei* (Sprengel) O'Donell, Lilloa 29: 69. 1959.

Exogonium umbellatum Moçiño & Sessé ex Choisy in DC., Prodr. 9: 336. 1845, nom. pro syn.

3. *Ipomoea neei* (Sprengel) O'Donell, Lilloa 29: 69. 1959.

Exogonium corimbosum Sessé & Moçiño ex O'Donell, Lilloa 29: 71. 1959, nom. pro syn.

A fourth species was not included in O'Donell's discussion of the *Quamoclit* group. The species is an *Ipomoea*; the flowers appear to be bird pollinated; and the morphology indicates affinity with the *Quamoclit* group.

4. **Ipomoea uhdeana** (Fenzl. ex Hall. f.) D. Austin, comb. nov.

Basionym: *Exogonium uhdeanum* Fenzl. ex Hall. f., Bot. Jahrb. Syst. 16: 559. 1893. A new name for *Quamoclit tubulosa* Mart. & Gal.

Synonyms: *Quamoclit tubulosa* Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 12: 270. 1845. TYPE: *Galeotti 1393* (W, isotype). *Ipomoea tubulosa* (Mart. & Gal.) Hemsl., Biol. Centr. Amer., Bot. 2: 395. 1882, non Roem. & Schult., 1819.

Group 5. *Ipomoea bracteata*, the type species of *Exogonium*, shares many characteristics with *I. purga* and its allies. Only three of the nine species in the alliance have been placed in *Exogonium*.

Ipomoea: *Exogonium* alliance.

Exogonium Choisy, Mem. Soc. Phys. Genève 6: 443. 1834.
Ipomoea subgen. *Exogonium* (Choisy) Meisn. in Mart., Fl. Bras. 7: 221. 1869.
Ipomoea sect. *Batatas* subsect. *Emeticae* House, Ann. New York Acad. Sci. 18: 239. 1908.

1. *Ipomoea bracteata* Cav., Icon. Descr. Pl. 5: 51, *pl. 477*. 1799. TYPE: Cited as *Ipomoea ?bracteata* by Cav.; based on two collections: Mexico, "Mazatlan duabus leucis" *Sessé & Moçiño* and "quattuor a Chipalcingo" *Sessé & Moçiño* (probably MA, not seen). Interpretation based on plate 477 by Cavanilles.

Synonyms: *Ipomoea cincta* Roem. & Schult., Syst. Veg. 4: 254. 1819, nom. illeg. *Exogonium bracteatum* (Cav.) Choisy, Mem. Soc. Phys. Genève 6: 443. 1834.

Ipomoea spicata H.B.K., Nov. Gen. Sp. Pl. 3: 112. 1819. TYPE: Mexico, *Humboldt & Bonpland* (P, not seen, microfiche seen). *Exogonium spicatum* (H.B.K.) Choisy, Mem. Soc. Phys. Genève 8: 128. 1838, nom. illeg.

Exogonium olivae Bárcena, Viaje Cav. Cacahuam. 29. 1874. TYPE: Mexico, Cuernavaca, *Bárcena* (presumably MEXU, not found). Interpretation based on the Bárcena plate.

Convolvulus bractiflorus Sessé & Moçiño, Pl. Nov. Hisp. 38. 1887; Pl. Nov. Hisp. 22. 1893. TYPE: Mexico, *Sessé & Moçiño* (probably MA). Their Icones 207 is cited in the 1893 publication, but I have not been able to obtain a copy of this. The interpretation used here is based on the protologue.

Ipomoea bracteata var. *pubescens* Robinson & Greenman, Amer. J. Sci. 50: 160. 1895. TYPE: Mexico, Jalisco, *Pringle 4734* (MO, holotype). *Exogonium bracteatum* var. *pubescens* (Robinson & Greenman) House, Bull. Torrey Bot. Club 35: 101. 1908.

Distribution: Baja California, Jalisco, Sinaloa, Oaxaca, Tepic, Morelos, Sonora, Chihuahua, Michoacán, and Guerrero (Mexico).

2. *Ipomoea dumosa* (Benth.) L. O. Williams, Fieldiana, Bot. 32: 190. 1970.
Basionym: *Exogonium dumosum* Benth., Pl. Hartw. 46. 1840. TYPE: *Hartweg s.n.* (K, holotype, not seen; F, photo).
Distribution: Mexico.
This species is very close to *I. purga* and has been considered synonymous with that population by some.

3. *Ipomoea elongata* Choisy in DC., Prodr. 9: 355. 1845. TYPE: Mexico, Oaxaca, *Andrieux 212* (G-DC, holotype; US, photo).
Distribution: Mexico. See Matuda, Anales Inst. Biol. Univ. Nac. México 35: 75. 1964.

4. *Ipomoea emetica* Choisy in DC., Prodr. 9: 376. 1845. TYPE: Mexico. Based on an unpublished plate by Sessé & Moçiño (not found).

Synonyms: *Ipomoea sagittata* Sessé & Moçiño ex Choisy in DC., Prodr. 9: 376. 1845, nom. pro syn., non Poir., 1791.
Ipomoea caudata Fernald, Proc. Amer. Acad. Arts 36: 498. 1901. TYPE: Mexico, Morelos, *Pringle 8448* (GH, holotype).

Distribution: Mexico. See Matuda, Anales Inst. Biol. Univ. Nac. México 36: 85. 1965.

5. *Ipomoea hintonii* L. O. Williams, Econ. Bot. 24: 400. 1970. TYPE: Mexico, *Hinton et al. 8474* (F, holotype).
Distribution: Mexico.

6. *Ipomoea purga* (Wender.) Hayne, Arzneigewächse 12: *tab. 33, 34.* 1833.
Basionym: *Convolvulus purga* Wender., Pharm. Central-Blatt 1: 457. 1830. TYPE: Based on plants grown from seed collected in Mexico by Schiede, probably not preserved. Interpretation based on Hayne plates.

Synonyms: *Exogonium purga* (Wender.) Benth., Pl. Hartw. 46. 1840.
Ipomoea schiedeana Zucc., Flora 14: 801. 1831. TYPE: Based on plants collected in Mexico by Schiede and cultivated by Zuccarini. Probably based on the same Schiede collections as *I. purga*.

Distribution: Mexico, Guatemala, El Salvador, Honduras, Costa Rica, Panama.

7. *Ipomoea seducta* House, Ann. New York Acad. Sci. 18: 241. 1908. TYPE: Guatemala, Alta Verapaz, *Tuerckheim 7926* (GH, US, isotypes).
Distribution: Mexico, Guatemala. See Standley & Williams, Fieldiana, Bot. 24 (9): 51. 1970.

8. *Ipomoea suffulta* (H.B.K.) G. Don, Gen. Syst. 4: 276. 1838.
Basionym: *Convolvulus suffultus* H.B.K., Nov. Gen. Sp. Pl. 3: 102, *pl. 211.*

1819. TYPE: Mexico, Volcán de Jorullo, *Humboldt & Bonpland* (P, not seen, microfiche seen).

9. *Ipomoea urbinei* House, Muhlenbergia 3: 41, *pl. 2. fig. b.* 1907. TYPE: Mexico, Volcán de Colima, *Bárcena 214* (presumably MEXU, not found).

Distribution: Known only from the type collection. See Matuda, Anales Inst. Biol. Univ. Nac. México 35: 67. 1964.

Group 6. The species in this group form a relatively homogeneous assemblage within *Eriospermum* which is normally recognized as a section or subgenus of *Ipomoea* (Verdcourt, 1963; Austin 1975a). Comose seeds separate these species from the others that have been placed in *Exogonium*. Some justification for the separation of this group from *Eriospermum* could be made. Most of the species listed here are adapted for bird pollination while others in *Eriospermum* are bee pollinated. If the two groups were placed in different taxa, several species-pairs (e.g., *I. eggersii*/*I. steudelii* and *I. viridiflora*/*I. carolina*) would be separated. While closely related, one species of these pairs conforms to the bee-pollination syndrome (*I. eggersii*), and the other to the bird-pollination syndrome (*I. steudelii*). If this alliance were separated from *Eriospermum*, the closely related species of the pairs would be placed in separate taxa.

Ipomoea mirandina/*I. microdactyla* alliance.

Exogonium Choisy, Mem. Soc. Phys. Genève 6: 443. 1834, in part, excl. type species.
Ipomoea sect. *Exogonium* (Choisy) Griseb., Fl. Brit. W. I. 472. 1862, excl. type species.

1. *Ipomoea argentifolia* A. Rich. in Sagra, Hist. Cuba 11: 131. 1850. TYPE: Isle of Pines, *Richard* (P, not seen).

Synonyms: *Exogonium argentifolium* (A. Rich.) House, Bull. Torrey Bot. Club 35: 102. 1908.

Ipomoea praecox Wright in Sauv., Fl. Cubana 107. 1873; Anales Acad. Ci. Méd. Habana 7: 46. 1870. TYPE: *Wright 3644* (US, isotype).

Distribution: Cuba, Isle of Pines, Mexico (Oaxaca, Puebla).

Although I have not seen the type of Richard's species, it is the only population on the Isle of Pines matching the protologue. The distribution of this species is worthy of note in that the plants are disjunct from western Cuba to the western slopes of the Sierra Madre Occidental in Mexico. The species is probably native to Cuba and not introduced since the allied species *Ipomoea lachnea* Sprengel (*Bertero*, MO, isotype) occurs in the Dominican Republic.

2. *Ipomoea carolina* L., Sp. Pl. 160. 1753. TYPE: Based on illustration in Catesby, Nat. Hist. Carolina 2: 9, *tab. 91* (lectotype).

Synonyms: *Exogonium pedatum* Choisy, Mem. Soc. Phys. Genève 8: 130. 1838. TYPE: Santo Domingo, *Poiteau* (G-DEL, not seen).

?*Ipomoea clausa* Rudolphi ex. Ledeb. & Adlerstam, Pl. Doming. 14. 1805; Ledeb., Neues J. Bot. 2: 292. 1807. TYPE: *Rudolphi* coll.? (not in LE).

Distribution: Haiti, Dominican Republic, Bahama Islands.

The synonymy listed here is based entirely on the descriptions since the types have not been seen. The protologue of *I. clausa* is general enough that one cannot be sure of the species. Some have thought that this name applies to *I. triloba*

(Matuda, 1965: 100). Perhaps *I. clausa* does apply to that species, but the description appears to me to better fit the population treated here as *I. carolina*. While I was in Geneva I looked for the type of *E. pedatum* but did not find it. Additional searching will perhaps solve that problem of synonymy.

3. *Ipomoea conzattii* Greenman, Publ. Field Columbian Mus., Bot. Ser. 2: 258. 1907. TYPE: Mexico, *Conzatti 1666* (F, holotype).

Synonym: *Exogonium conzattii* (Greenman) House, Bull. Torrey Bot. Club 35: 102. 1908.

Distribution: Mexico (Guerrero).

4. **Ipomoea concolora** (Matuda) D. Austin, comb. nov.
Basionym: *Exogonium concolorum* Matuda, Anales Inst. Biol. Univ. Nac. México 36: 116. 1965 (1966). TYPE: *Kruse 844* (MEXU, holotype).

5. *Ipomoea clarensis* Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22: 121. 1955. TYPE: Cuba, *Leon & Roca 7959* (NY, holotype, not found). Although the type was not found, there is a specimen [*Howard 6565* (US)] annotated by Alain.

Distribution: Endemic to Cuba. This species is very similar to *I. microdactyla*. The main difference is the flower color: red in *I. microdactyla* and white in *I. clarensis*.

6. *Ipomoea cubensis* (House) Urban, Symb. Antil. 9: 427. 1925.
Basionym: *Exogonium cubense* House, Bull. Torrey Bot. Club 35: 105. 1908. TYPE: *Britton & Shaffer 495* (NY, holotype).

7. *Ipomoea desrousseauxii* Steud., Nom. Bot., ed. 2. 816. 1841. TYPE: Based on *Convolvulus eriospermus* Desr.
Basionym: *Convolvulus eriospermus* Desr. in Lam., Encycl. Méth. Bot. 3: 567. 1789. TYPE: probably in P-LAM, not seen.

Synonyms: *Exogonium eriospermum* (Desr.) Choisy, Mem. Soc. Phys. Genève 8: 130. 1838. *Ipomoea eriosperma* (Desr.) Raf., Fl. Tell. 4: 74. 1838, non Beauv., 1807.

The specimen in the DeCandolle herbarium [Santo Domingo, *Bertero s.n.* (G-DC)] matches the description of Desrousseaux and the synonymy is based on that specimen.

Distribution: Santo Domingo.

8. **Ipomoea eggersii** (House) D. Austin, comb. nov.
Basionym: *Exogonium eggersii* House, Bull. Torrey Bot. Club 35: 104. 1908. TYPE: St. Thomas, Feb. 1887, *Eggers* (NY, holotype, not found; G, L, isotypes).
Distribution: St. Thomas, Tortola.

This species has been confused with *I. steudelii*. Differences between them are few; the major distinction is that *I. eggersii* has white bee-pollinated flowers and *I. steudelii* has red bird-pollinated flowers.

9. *Ipomoea fuchsioides* Griseb., Cat. Pl. Cub. 205. 1886. TYPE: Cuba, *Wright 3095* (MO, isotype).

Synonyms: *Exogonium fuchsioides* (Griseb.) House, Bull. Torrey Bot. Club 35: 101. 1908.

Distribution: Endemic to Cuba.

10. *Ipomoea incerta* (Britton) Urban, Symb. Antil. 9: 247. 1924.
Basionym: *Exogonium incertum* Britton, Mem. Torrey Bot. Club 16: 94. 1920. TYPE: Cuba, *Shafer 1235* (NY, holotype).
Distribution: Endemic to Cuba.

11. *Ipomoea jalapoides* Griseb., Cat. Pl. Cub. 202. 1886. TYPE: Cuba, *Wright 3097* (MO, isotype).

Synonym: *Exogonium jalapoides* (Griseb.) House, Bull. Torrey Bot. Club 35: 101. 1908.

Distribution: Endemic to Cuba.

12. *Ipomoea longistaminea* O'Donell, Lilloa 23: 488. 1950. TYPE: Brasil, Bahia, *Rose & Russell 19784* (US, holotype).
Distribution: Endemic to Brasil and apparently to the state of Bahia.

13. *Ipomoea leuconeura* Urban, Symb. Antil. 3: 350. 1902. SYNTYPES: Haiti, *Ehrenberg 134* (US, fragment), *Picarda 16* (US, fragment), *Buch 5* (not seen).

Synonym: *Exogonium leuconeurum* (Urban) House, Bull. Torrey Bot. Club 35: 106. 1908.

Distribution: Endemic to Haiti.

14. *Ipomoea microdactyla* Griseb., Cat. Pl. Cub. 204. 1886. TYPE: Cuba, *Wright 3094* (MO, isotype).

Synonyms: *Exogonium microdactylum* (Griseb.) House, Bull. Torrey Bot. Club 35: 102. 1908.
Exogonium microdactylum var. *integrifolium* House, Bull. Torrey Bot. Club 35: 103. 1908. TYPE: Cuba, *Wright 3102* (MO, isotype).
Ipomoea repanda sensu Griseb., Cat. Pl. Cub. 204. 1886, non Jacq., 1760.

Distribution: Florida, Bahamas, Cuba. These vines are found only in the rocky pinelands of Dade and Monroe counties in Florida. In the Bahamas (Inagua) the Bahama Woodstar hummingbird visits and pollinates the flowers.

15. *Ipomoea mirandina* (Pittier) O'Donell, Lilloa 26: 370. 1953.
Basionym: *Exogonium mirandinum* Pittier, J. Wash. Acad. Sci. 21: 143. 1931. TYPE: Venezuela, *Pittier 12217* (VEN, holotype; US, isotype).
Distribution: Known from Venezuela and Panama; undoubtedly in Colombia also but no specimens seen.

16. *Ipomoea repanda* Jacq., Enum. Pl. Carib. 13. 1760; Sel. Stirp. Amer. 28, *pl. 20.* 1763, non Griseb., 1886. LECTOTYPE: illustration by Jacquin, *pl. 20.* 1763.

Synonyms: *Convolvulus repandus* (Jacq.) Desr. in Lam., Encycl. Méth. Bot. 3: 555. 1789. *Exogonium repandum* (Jacq.) Choisy, Mem. Soc. Phys. Genève 8: 128. 1838.

Distribution: Puerto Rico, Tortola, Cuba, Barbuda, Antigua, Martinique, Dominica, Guadeloupe, St. Vincent, Montserrat, St. Lucia, St. Jan.

17. **Ipomoea retropilosa** (Pittier) D. Austin, comb. nov.
Basionym: *Exogonium retropilosum* Pittier, J. Wash. Acad. Sci. 21: 143. 1931. TYPE: Venezuela, Mérida, *Pittier 12698* (VEN, holotype; MO, US, isotypes).
Distribution: Endemic to the coastal mountains of Venezuela.

18. **Ipomoea shinnersii** D. Austin, nom. nov.
Basionym: *Exogonium luteum* House, Bull. Torrey Bot. Club 35: 103. 1908. TYPE: Mexico, *Conzatti & Gonzalez 668* (GH, holotype; NY, isotype).
Because of *Ipomoea lutea* Hemsley (Diagn. Pl. Nov. 34, *tab. 60.* 1878) a new name is required for House's species. The new name commemorates the late Lloyd Shinners, a student of Convolvulaceae.
Distribution: Mexico. (Guerrero).

19. **Ipomoea shinnersii** var. **woronovii** (Standley) D. Austin, comb. et stat. nov.
Basionym: *Exogonium woronovii* Standley, Field Mus. Nat. Hist., Bot. Ser. 11: 171. 1932. TYPE: Mexico, *Woronow 2906* (F, holotype).
Distribution: Mexico (Michoacán).

20. *Ipomoea signata* House, Muhlenbergia 3: 46. 1907. TYPE: Guatemala, *Nelson 3595* (US, holotype).
Distribution: Mexico, Guatemala, Venezuela. See Matuda, Anales Inst. Biol. Univ. Nac. México 35: 72. 1964; Standley & Williams, Fieldiana, Bot. 24 (9): 53. 1970. The distribution of this species is unusual in that it appears to be absent from a large part of Central America and reappears in the coastal mountains of Venezuela.

21. *Ipomoea steudelii* Millsp., Publ. Field Columbian Mus. Nat. Hist., Bot. Ser. 2: 86. 1901. TYPE: Based on *Ipomoea arenaria* (Choisy) Steud.

Synonyms: *Exogonium arenarium* Choisy, Mem. Soc. Phys. Genève 8: 129, *pl. 1.* 1838. TYPE: Puerto Rico, *Bertero* (G-DC, lectotype). *Ipomoea arenaria* (Choisy) Steud., Nom. Bot., ed. 2. 815. 1841, non Roem. & Schult., 1819.
Ipomoea eggersiana Peter in Engler & Prantl, Nat. Pflanzenfam. IV (3a): 30. 1891, nom. nud.

Distribution: Puerto Rico, St. Croix, Virgin Gorda, St. Thomas, St. John.
Choisy based *Exogonium arenarium* on four collections. These collections came from Puerto Rico, St. Thomas, Santo Domingo, and the Bahamas. According to the interpretation that has been used for the past 60 to 70 years, the species does not occur on either the island of Hispaniola or in the Bahamas. Therefore, neither of the collections cited by Choisy from these islands should be chosen as the type. The specimen in Geneva matches the concept of historic use and has been chosen to be the lectotype.

22. **Ipomoea avicola** D. Austin, nom. nov.
Basionym: *Exogonium verruculosum* Pittier, J. Wash. Acad. Sci. 21: 142. 1931. TYPE: Venezuela, Aragua, *Pittier 12118* (VEN, holotype; G, US, NY, isotypes).

Synonym: *Ipomoea verruculosa* (Pittier) O'Donell, Lilloa 26: 379. 1953, non *I. verruculosa* Mart. ex Choisy in DC., Prodr. 9: 378. 1845, nom. pro syn.

Distribution: Endemic to the coastal mountains of Venezuela.

This and the Brasilian *I. longistaminea* O'Donell are similar. These two populations apparently represent local endemic bird-pollinated flowers derived independently.

23. *Ipomoea viridiflora* Urban, Symb. Antil. 3: 348. 1902. TYPE: *Ehrenberg 345* (US, isotype).

Synonym: *Exogonium viridiflorum* (Urban) House, Bull. Torrey Bot. Club 35: 106. 1908.

Distribution: Cuba, Hispaniola.

Group 7. These two species belong to different alliances within the *Eriospermum* group of *Ipomoea*. Flowers on the plants are apparently bee pollinated and the inclusion of these species in *Exogonium* appears anomalous.

1. *Ipomoea argentea* Meisn. in Mart., Fl. Bras. 7: 247. 1869. SYNTYPES: Brasil, *Gardner 3356* (not seen). Venezuela, *Spruce 3605* (K).

Synonyms: *Ipomoea comosa* House, Ann. New York Acad. Sci. 18: 201. 1908. TYPE: Based on *I. villosa* (Choisy) Meisn. *Batatas villosa* Choisy in DC., Prodr. 9: 337. 1845. TYPE: Brasil, *Martius 609* (M, syntype). *Ipomoea villosa* (Choisy) Meisn. in Mart., Fl. Bras. 7: 244. 1869, non Ruiz & Pavon, 1799. *Exogonium villosum* (Choisy) Peter in Engler & Prantl, Nat. Pflanzenfam. IV (3a): 28. 1891.

Distribution: Known from savannas in Venezuela, south to Brasil. The plants show considerable variation throughout the range, prompting the division of the population. O'Donell (1960) was one of the first to point out that they were the same.

2. *Ipomoea steerei* (Standley) L. O. Williams, Fieldiana, Bot. 32: 195. 1970. Basionym: *Exogonium steerei* Standley, Carnegie Inst. Wash. 461: 83. 1935. TYPE: *Steere 1545* (F, lectotype). *Steere 1599* (F, syntype).
Distribution: Reported from Mexico and Guatemala.

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THE *LUPINUS MONTANUS* COMPLEX OF MEXICO AND CENTRAL AMERICA[1]

David B. Dunn[2] and William E. Harmon[3]

Abstract

The recognition of the *Lupinus montanus* complex by morphological traits is discussed. Ecological modification of traits is discussed and the island nature of distribution from mountain peak to mountain peak produces semi-isolated gene pools. Long range dispersal and introgression from other lupines has occurred at the northern end of the distribution in San Luis Potosí, Mexico, developing *L. cacuminus*. A similar situation occurred in Costa Rica, with *L. valerioi* the product of introgression from, as yet, an unknown taxon. In Guatemala var. *austrovolcanicus* represents local introgression from *L. kellermanianus*, into *L. montanus*. Both of the Peruvian (*L. praestabilis* and *L. proculaustrinus*) taxa are, likewise the result of long range dispersal and introgression. The geographic range of each of the taxa of the complex is plotted and the interrelationship is discussed. The alkaloids have been plotted from random samples of each of the taxa and the data supports the taxonomic treatment and interpretation of their interrelationship.

The lupines of Mexico have never been studied monographically. Previous studies have been floristic for states or regions or miscellaneous descriptions, as contributions to the flora of Mexico. To avoid further nomenclatural complications, the earliest named taxa should be identified first. In this sense, the first taxon named for Mexico was *Lupinus mexicanus* Cerv. ex. Lag. (1816), which has been identified (Dunn, 1972). *Lupinus montanus* H.B.K. (1823) was the second epithet published for Mexico, concurrently with *L. elegans* H.B.K. (Humboldt et al., 1823: 478). Both of the types of these taxa are available at Paris, France, with microfiche illustrations now widely distributed. The topotype material was studied and dissections of 50 collections, representing the geographic range of *L. montanus* were made, and the mean measurements were used to prepare the illustrations of *L. montanus* and allies presented in this paper. The illustration of *L. montanus* was sent to Paris and the curator of the herbarium kindly varified that the illustration accurately represents the species by matching it with the type specimen. Since *L. elegans* H.B.K. is the first epithet in a different complex of lupines, it will be treated, as soon as the rest of the complex is understood. With this approach it is believed, after ten years of study of the Mexican lupines and dissection of over 100 types for Mexico, that the taxonomic treatment of the *L. montanus* complex for Mexico and Central America can be presented. C. P. Smith (1948: 608) reported two South Ameri-

[1] The authors wish to express appreciation to the multiple curators of herbaria who loaned material for the study, as cited in the distributions by the code letters from *Index Herbariorum* (Holmgren & Keuken, 1974). Special appreciation is expressed to the curators at Paris for comparing the illustration prepared for *L. montanus* with the type specimen. Two additional herbaria are cited which were not in the code. CUN = University of Northern Colorado, Greeley, Colorado, U.S.A., and WUP = Wisconsin University–Platteville, Platteville, Wisconsin, U.S.A.

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can species to belong to what he interpreted as the "*Lupinus montanus* complex." Only one of these was available for study. It is a member of the complex and is very distinctive in multiple characteristics. Both are only treated in the key.

Morphological Recognition

Lupinus montanus, per se, can be readily identified by the large sheathing *stipules*, the largest per specimen being 3–33 cm long. The infraspecific taxa show various modifications of the shape, size, texture, and vestiture of the stipules. (The allies are so different that they cannot be recognized by the stipules.) The *stems*, 0.5–2.5 m tall (to 4 m shrubs in Peru), are clustered from a woody caudex, and in age become short woody trunks, to 5 cm diameter. The current year's growth is normally hollow and fistulose or subfistulose, varying from 5–30 mm in diameter. (Allies and products of introgression have woody, solid stems, as small as 3 mm in diameter, and are only 3–7 dm tall.) The *leaves* show no general relationship other than a tendency to have many (9–17) leaflets, palmately compound, linear-elliptic to oblanceolate and generally glabrous above, but the last trait is modified by increasing hairiness above, with higher elevations and by introgression from the allies. The *flower structure* shows the greatest degree of uniformity, with only very subtle changes in size, shape and vestiture of the calyx, and size and position of the bracteoles. Keels are generally glabrous but both infraspecific taxa and the allies may have ciliate keels. The base of the deep sulcus of the banner appears to have a nectary, which is uncommon in *Lupinus*. The number of ovules varies from taxon to taxon, with *L. montanus* and the infraspecific taxa varying from 7–13 per pod (the allies less). The seeds of *L. montanus* and the infraspecific taxa are very similar in shape to those of *L. polyphyllus*, a species distributed from southern California to British Columbia, with which it has been confused. The seeds are generally 4.5 mm long and 3 mm wide, with a deep funicular pit at the side of one end.

While the large stipules represent the most distinctive trait of the *L. montanus* complex, they are very small in some of the allies and reduced in taxa considered to be products of introgression. The large flowers with the banners reflexing near the midpoint are perhaps the most consistent character of the complex. They may indicate the utilization of specific pollinators.

Habitat and Ecological Modifications

The taxa of the complex are associated with the upper forest openings extending upward to timberline. Thus the population on each mountain represents a breeding population with a chance for some genetic drift or fixation. This is reflected by variations in the hair type from mountain to mountain. However, to view the population on each mountain as having achieved some taxonomic status would be an exaggeration. It appears probable that migratory birds contribute to the separated populations of each mountain peak intermittently. There is also an altitudinal modification of the density of pubescence of both the stems and leaflets. On Popocatepetl the smallest specimens were at the lowest altitude

and the area above timberline. The largest specimens were within the upper margins of timber. The densest pubescence was at the highest elevation and the sparsest pubescence was at the lower elevation, with the leaflets glabrous above at the lower elevations. On Nevada de Toluca, the type locality, the situation was similar. Sharma (1967, in an unpublished part of his thesis) demonstrated experimentally that hair frequency increased with aridity and heat. The vegetative stature of the plants within the complex ranges from 0.3–2.5 m in height, while those within *L. montanus* vary from 0.5–2.5 m tall.

Evolution and Geographical Relationships (Fig. 1)

Lupinus muelleri and *L. kellermanianus*, treated here as allies, can be utilized to illustrate both the islandlike mountain isolation and long range disjunction of taxa with morphological similarities. The two are very closely related, but *L. kellermanianus* is known only from two volcanic peaks in Guatemala, while *L. muelleri* is known only from the opposite end of the distributional range of the complex on Cerro Potosí, Nuevo León, Mexico. Vegetatively they are very different from the rest of the *L. montanus* complex, having woody stems, low (3–5 dm) stature, only 2–2.5 cm long petioles, only 2–2.5 cm long leaflets with strigose-sericeous pubescence on both sides, and only 8–20 mm long stipules. The flowers, however, are very similar to *L. montanus* except that both are pubescent on the back of the banner. The vegetative traits, except pubescence, resemble *L. argenteus* of the Rocky Mountains of the United States but the closest geographic approach of this species is in northern New Mexico, while *L. muelleri* occurs in southern Nuevo León and disjunctly in Guatemala, where *L. kellermanianus* also occurs. The pubescence of the leaflets and the banner resembles that of the *L. sericeus* complex, but the closest approach of this complex is in northern Arizona, north of the Grand Canyon. If the source of the characteristics is from the above two complexes of the United States, then long range dispersal seems the only plausible explanation, via migratory seed-eating birds. *Lupinus muelleri* is on a mountain ridge surrounded by Chihuahuan desert, but inhabits the lower pine zone. *Lupinus kellermanianus* was collected high on Volcán Agua near timberline, hence both are in somewhat xeric situations where abundant pubescence is adaptive.

Introgressive Hybridization

Lupinus cacuminus is vegetatively intermediate between *L. muelleri*, with which it has geographic proximity, and *L. montanus*, from which it is geographically completely isolated. *Lupinus cacuminus* has intermediate stipules, leaflets, and petioles, the fistulose stems of *L. montanus*, but the pubescent banner of *L. muelleri*, and extends above timberline, an ecological trait of *L. montanus*. In some populations of *L. cacuminus* an intermediate amount of ciliation occurs on the keel, a trait derived from *L. muelleri*. The multiple collections are very similar and appear to be a stabilized entity, derived from the hybridization of the *L. montanus* genome with the *L. muelleri* genome. The alkaloid spectrum of *L. cacuminus* is identical with that of *L. montanus* as shown below.

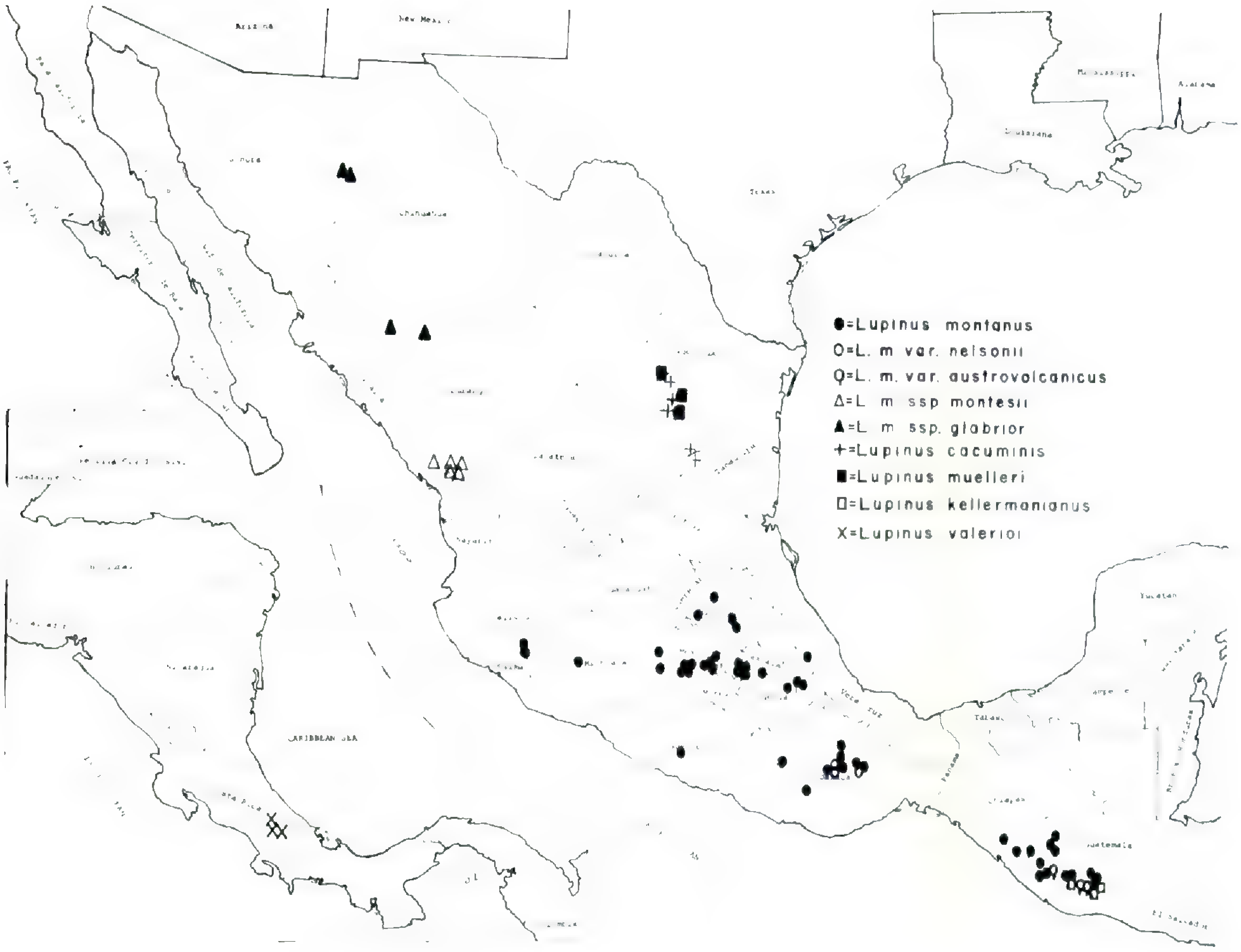

FIGURE 1. Distribution of the taxa of the *Lupinus montanus* complex and their allies in Mexico and Central America.

Lupinus montanus subsp. *montanus* var. *austrovolcanicus* may be the product of introgression between ancestral *L. montanus* and *L. kellermanianus*. In this case *L. kellermanianus* could have provided the woody stem, reduced stature, and intermediate vegetative traits. Both *L. kellermanianus* and *L. montanus* var. *austrovolcanicus* are limited to one or two mountain peaks and have only been collected a few times. It is thus questionable whether the process of introgression has progressed long enough to have established a stabilized taxon of intermediate appearance.

Another possible example of a long range introduction of some portion of the *L. montanus* genome into a lupine population is provided by *L. valerioi* on Cerro Vueltas in Costa Rica. There is a long distance between this population and the nearest known material of *L. montanus* in Guatemala. In this case the stipules are intermediate in size, somewhat similar to those of *L. cacuminus*. The bracts, however, are quite large and broad, typical of *L. montanus*. The stems are very slender, similar to those of *L. kellermanianus*, but the petioles are long, 6–12 cm, and have spreading pilose hairs to 4 mm long. These traits all suggest a mixing of genetic traits of *L. montanus* with some, as yet undetermined taxon of *Lupinus*. None presently known from Costa Rica provides these characteristics.

A fourth example of long range introduction of genetic material from the

L. montanus genome is provided by *L. proculaustrinus* C. P. Smith of Peru. In this case the plants have retained many of the traits of *L. montanus*, including the large sheathing stipules and large broad bracts. The species has multiple unique traits, however, which are not present in *L. montanus*. A conspicuous one is the glabrous, glaucous surface and also a shrubby stature, reported on some specimens to be up to 4 meters in height. The other Peruvian species, *L. praestabilis* C. P. Smith has not been available for study.

ALKALOID CHEMISTRY

The material utilized was dried leaflets in all cases, since we have observed some cases where the alkaloids stored in the seeds were different from those present in the leaves. Seed material is not always present. Four to five leaflets were fragmented in a new coin envelope for each sample and transferred to a test tube. In species with large leaflets only one is necessary. Enough 30% KOH was added to wet the leaf fragments. Enough chloroform was added to cover the fragments. The rack with the test tubes was then stored in a refrigerator for one day (24 h). A micropipette was utilized to spot 50 μl of the clear chloroform solution from the bottom of the test tube, for each sample, onto a thin-layer chromatographic plate (TLC). If no clear bottom layer was present, a few drops of chloroform was added to the test tube. The solvent utilized to separate the alkaloids was 95 parts chloroform, 4 parts anhydrous methyl alcohol, and 1 part ammonium hydroxide, by capillary flow, against gravity, in a Brinkman tank. The flow was stopped at 15 cm and the plate dried and developed first with Dragendorf's reagent. All visible spots were marked with a pencil. The plate was then sprayed with iodaplatinate to bring out any trace substances not observed with the first stain. The R_f values plotted in Table 1 have been correlated with standards supplied by Cho & Martin (1971) for sparteine, lupanine, hydroxylupanine and cytisene, on each plate that was prepared.

While the number of samples plotted is not large, it is quite clear that while some variation occurs in the trace alkaloids, the presence of the principal alkaloids is fairly consistent. Within *L. montanus* both varieties retain the same principal alkaloids, while the two subspecies show distinct alterations in the principal alkaloids. The suggestion that *L. kellermanianus*, *L. valerioi*, and *L. cacuminus* are allied is supported by the fact that the samples analyzed show the same principal alkaloids as those in *L. montanus* proper.

Lupinus muelleri has a distinctly different spectrum of alkaloids from *L. cacuminus* suggesting that the two taxa are maintaining their isolation at the present time, even though they are in close proximity and are separated only altitudinally by a few hundred feet.

The lone specimen available from Volcán Colima, probably in Jalisco, suggests that this population may be sufficiently isolated to require recognition. However, a single sample is not sufficient to permit an analysis of the situation, particularly since it appears to be morphologically very little different from the main population of *L. montanus*, even though it is geographically isolated.

TABLE 1. *Lupinus* specimens tested for the presence of alkaloids. Sparteine, R_f 0.08, and lupanine, R_f 0.72, were used on each plate to standardize the results. T = trace amount; + = small amount; ++ = moderate amount; +++ = large amount.

Taxon	R_f Values for Alkaloids																						
Locality and Voucher	0.00	0.01	0.02	0.05	0.08	0.11	0.12	0.13	0.15	0.16	0.22	0.23	0.28	0.42	0.46	0.56	0.61	0.67	0.69	0.72	0.79	0.81	0.87
Lupinus muellerii																							
Nuevo León, Las Canoas, *Mueller 2205*		T		+																++			
Nuevo León, Cer. Potosí, *Beaman 3311*				+												+							
Lupinus cacuminus																							
Coahuila, Los Alpes, *Gentry 20059*	+	T			+++																		
Nuevo León, C. Potosí, *Beaman 2654*	+	T			+++																		
Nuevo León, C. Potosí, *Ill. Exp. 958*	+	T			+++																		
Nuevo León, C. Potosí, *McGregor 314*	+	T			+++																		
Nuevo León, Peña Nev., *Beaman 2690*	+	T			+++												T						
Tamaulipas, Peña Nev., *Stanford 2597*	+	T			+++																		
Lupinus montanus subsp. *montanus* var. *montanus*																							
Chiapas, Mt. Pasitar, *Matuda 70*	+				+++																		
Guatemala, Atitlán, *Beaman 4094*	T	T	T		+++																		
Guatemala, Vol. Agua, *Harmon 3646*					+++																		
Guatemala, Chaucol, *Nelson 3641*	++	T	T	T	+++					T													
Oaxaca, *Hallberg 790* and *931*	+	T	T		+++																		
Oaxaca, S. Juárez, *Matuda 38415*	+	+	T		+++								+			T				+	+		
Mexico, Popo', *Dunn 18558* + sev.	+				+++												T						
Mexico, S. Ajusco, *Garcia V1954*	+	+			+++																		
Jalisco, Nev. Colima, *Matuda 38369*	T	T			T								+++							+	++		
Lupinus montanus subsp. *montanus* var. *nelsonii*																							
Oaxaca, Llano Flores, *MacDougal 1960*	+		T		+++			T															
Oaxaca, Ixtlán, *Gentry 20272*	+		T		+++			T															
Oaxaca, Cer. Zemo', *Schultes 502*	+										T		T		T					T			
Lupinus montanus subsp. *montanus* var. *austrovolcanicus*																							
Guatemala, V. St. Mar., *Nelson 3709*	++	T	T	T	+++						T		T		T		T			T		T	
Guatemala, V. St. Mar., *Beaman 4124*	+	+	T	T	+++											T							
Guatemala, V. Tajumulo, *Plowman 3045*	+	T	T	T	+++																		
Lupinus montanus subsp. *montesii*																							
Durango, El Salto, *Waterfall 15490*				++	+																		
Durango, El Salto, *Waterfall 12714*	++			++	+																		
Durango, El Salto, *Guzman* Sep. 1961	++			++	+	+	T																
Durango, Pueblo N., *Maysvilles 8071*	T						T					T			++								
Lupinus montanus subsp. *glabrior*																							
Durango, S. Madre, *Nelson 4785*	T	T			++												++						
Durango, S. Madre, *Nelson 4785,2*	+	T			++									T		++	++						
Chihuahua, S. Madre, *Pringle 1206*	T						+										++			+		++	+
Lupinus kellermanianus																							
Guatemala, V. Zunil, *Steyermark 34848*	+	T	+	T	+++						T		T		T								
Guatemala, V. Agua, *Kellerman 15*	+	T	+	T	+++								T		T								
Lupinus valerioi																							
Costa Rica, *Burger & Liesner 7402*	+	T	+	T	+++						T		T		T								
C.R., Cor. Talamanca, *Weber 6257*	+	T	+	T	+++										T								
C.R., C. Vueltas, *Standley & Valerio 43974*	+	T	T	T	+++										T								
C.R., C. Vueltas, *Standley & Valerio 43668*	+	+	+	T	+++										T								
C.R., C. Frio, *Jiménez 2677*	+	T	+	T	+++				T						T								

TAXONOMY

KEY TO *Lupinus montanus* AND ALLIES

a. Banner sparsely strigose dorsally, near the distal half, along the crest; stipules 4.5 cm long or less (see also var. *australovolcanicus*); leaflets linear to linear-lanceolate, 2.5–5 cm long, strigose to sericeous above.
  b. Plants about 14 dm tall or more, glabrous or minutely puberulent; bracts persistent; known only from Peru .... (not treated) *L. praestabilis*
  bb. Plants 4–9 dm tall, sericeous to strigose; known from Guatemala or Mexico.
    c. Petioles 5–13 cm long; stems hollow, fistulose below; pubescence appressed-sericeous; Nuevo León, Mexico .... 2. *L. cacuminus*
    cc. Petioles 2–4.5 cm long; stems solid and ligneous.
      d. Keels glabrous; pubescence of leaflets strigose-sericeous; known from Guatemala .... 4. *L. kellermanianus*
      dd. Keels ciliate; pubescence of leaflets strigose-sericeous; known from Coahuila and Nuevo León .... 3. *L. muelleri*

aa. Banner glabrous; largest stipules more than 4.5 cm long or the stems with long spreading pilose hairs, 3–4 mm long; leaflets mostly glabrous above, sometime strigose above, variable in size up to 15 cm long.
  e. Pubescence of the stems with abundant spreading pilose hairs to 4 mm long; stems becoming ligneous; petioles 6–12 cm long; largest leaflets 4–7 mm long; known from Costa Rica .... 5. *L. valerioi*
  ee. Pubescence of the stems strigose, glabrous, or canescent; petioles variable in size; stems ligneous or herbaceous; largest leaflets 5–15 cm long; widely distributed.
    f. Stems and stipules glabrous to minutely puberulent; leaflets glabrous above; keels glabrous or sparsely ciliate above distally; known from Chihuahua, Durango, or Peru.
      g. Stems glabrous and glaucous; flowers 18–20 mm long; shrubs to 3.5 m tall; known only from Peru .... (not treated) *L. proculaustrinus*
      gg. Stems glabrous or glabrate; flowers 15–18 mm long; herbaceous stems 5–15 dm tall; known from northwestern Mexico.
        h. Bracts lance shaped, strigose dorsally; upper lip of the calyx truncate with an irregular notch; known from Chihuahua and northern Durango .... 1d. *L. montanus* subsp. *glabrior*
        hh. Bracts lanceolate, the tips attenuate and setaceous hairy, the lower dorsal area glabrous; upper lip of the calyx triangular; known from southwest Durango and Sinaloa .... 1e. *L. montanus* subsp. *montesii*
    ff. Stems, stipules, and bracts abundantly pubescent; known from other areas of Mexico and Guatemala.
      i. Stipules hispidulous to canescent within, the larget 10–33 cm long; stems fistulose, hispidulous to retrorsely hispidulous, 12–33 mm in diameter; known only from Ixtlán, Oaxaca, Mexico .... 1b. *L. montanus* subsp. *montanus* var. *nelsonii*
      ii. Stipules glabrous within, or if pubescent, not with the above combination of characteristics, generally less than 10 cm long; stems puberu-

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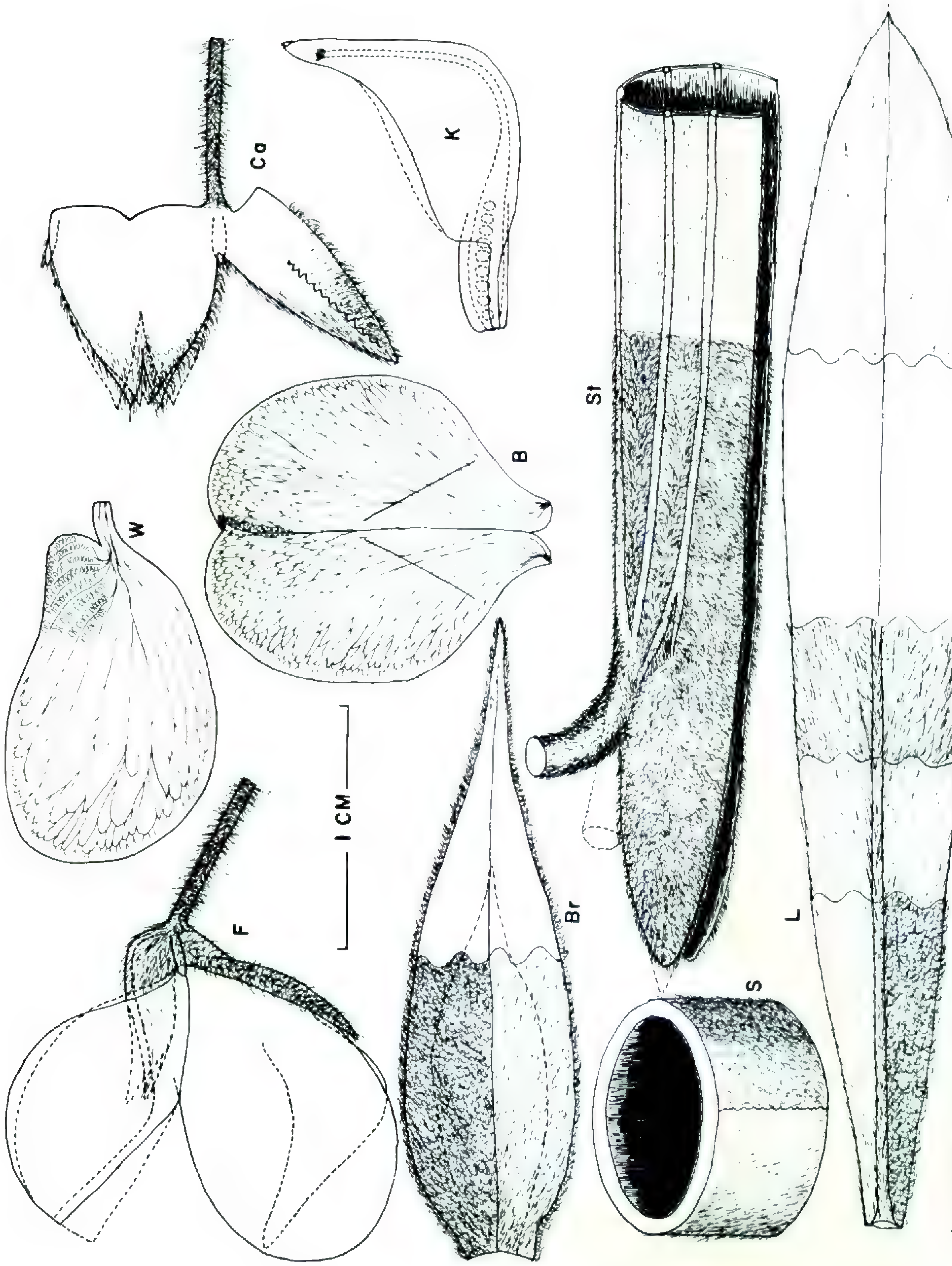
FIGURE 2. Illustration of the typical structures of *Lupinus montanus* subsp. *montanus* var. *montanus*. The floral and vegetative parts are drawn to the mean value of a set of 30 dissections from the geographic range of the taxon. The lettering is the same on all of the figures: F = lateral view of the left side of the flower; B = banner petal flattened, dorsal view; Br = bract, outside lower portion, inside upper portion; Ca = calyx, cut at the left lateral sinus and opened so that the inside is illustrated; K = keel petals, enclosing staminal tube and pistil, with the mean number of ovules drawn; L = average largest leaflet drawn to ½ the scale used for the floral part, the lower half shows different hair types observed on the lower surface, the upper half shows hair types observed on the upper surface; S = stem structure of first year growth and hair types, half scale; St = sheathing pair of stipules, half scale, showing hair types; W = wing petal.



Lupinus montanus H.B.K. (montanus)

lent to strigose or hispidulous, hollow, 4–12 mm in diameter on the first year's growth, becoming ligneous.

j. Stems to 4 mm in diameter, but hollow on the first year's growth, finely appressed puberulent; stipules only 2–4.5 cm long and pubescent within; racemes generally less than 8 cm long; rare, known from Volcán Santa María, Guatemala .... 1c. *L. montanus* subsp. *montanus* var. *austrovolcanicus*

jj. Stems of the first year's growth over 5 mm in diameter, hollow and flattening on pressing, variously pubescent; largest stipules 4–9 cm long, commonly glabrous over most of the area within; racemes over 15 cm long at maturity; known from Guatemala to central Mexico .... 1a. *L. montanus* subsp. *montanus* var. *montanus*

1a. **Lupinus montanus** H.B.K. subsp. **montanus** var. **montanus**, Nov. Gen. Sp. Pl. 6:477. 1823. TYPE: Mexico, Montosis Novae Hispaniae (Nevada de Toluca, 9,000–10,000 ft) (P, holotype, not seen; microfiche, MO).—FIG. 2.

L. vaginatus Cham. & Schlecht., Linnaea 5:590. 1830. TYPE: Mexico, Monte Orizaba, Sep., *Schiede & Deppe* (HAL, holotype; photos, NY, TEX, UMO).

L. flabellaris Bertol., Fl. Guat. 30. 1840. TYPE: Guatemala, Volcán d'Agua (not seen). TOPOTYPE: *Harmon 3646* (MO, NY, UC, UMO, US).

Plants perennial, 0.8–2 m tall, rarely to 2.5 m; stems hollow above the ground level, with the current year's growth 5–12 mm in diameter, pubescence varying with locality and altitude, finely appressed puberulent, to strigose or sericeous, more densely at higher altitudes, or hispidulous to retrorsely hispidulous or canescent; petioles of the primary leaves along the upper stems 6–15 cm long with the stipules connate nearly half the length of the petioles, those of dwarf lateral branches often reduced in size; stipules ensheathing ¾ or more of the diameter of the stems, 4–9 cm long, the triangular free tips 4–12 mm long, both petioles and stipules pubescent dorsally as the stems, the stipules generally glabrous or glabrate within, on dwarf branches the stipules of the multiple leaves imbricated; leaflets of the larger primary leaves 10–15, linear to narrowly oblanceolate, the largest 5–13 cm long, 5–14 mm wide, generally glabrous above at lower elevations and puberulent to strigose above at higher elevations, the tips acute or slightly attenuate; peduncles 10–22 cm long, shorter on late-season branches; racemes 15–30 cm long at maturity, verticillate to subverticillate; bracts large-sheathing or covering 3–5 cm of the tip of the elongating raceme, hiding the buds, the tips attenuate-caudate, pubescence as the stipules for each population, generally caducous; pedicels 5.5–8.4 mm long, hispid or with appressed hairs; calyces sericeous, strigose or canescent on the outside, puberulent within on the distal portion of both lips, the lower lip 8–11 mm long, generally entire, the upper lip 5.5–8.4 mm long, the notch at the tip 1–5 mm deep, the lips connate laterally 1.4–1.8 mm, the bracteoles 1.0–3.4 mm long, attached below the lips of the lateral sinuses; corollas glabrous, blue to lavender or purple, occasionally white or pink; banner obovate-rotund, longer than wide, the tip emarginate, 12.6–14.8 mm long, 11–14.5 mm wide, reflexed near the midpoint, reflexed 5.7–8 mm, appressed 6.7–7.8 mm, reflexed/appressed ratio 0.81–1.06, the angle 130°–146°; wings 13.8–16 mm long, 6–10 mm wide, the claw 2–3.7 mm long; keel 4–5 mm wide in the middle, the angle 84°–98° (average 90.9°); ovules 7–10; pods 4–5 cm long, 9–10 mm wide when dried, arching

up and outward, abundantly to sparsely tangled-pilose, the hairs 1–2.5 mm long; seeds black or brown with dark mottling, 4–4.5 mm long, 3–3.6 mm wide, with a deep funicular pit; chromosome number $n = 24$ (Beaman et al., 1962).

This is one of the wide-ranging species of the volcano zone of Mexico and Central America. It occupies a zone on most of the high mountains from timberline, or above in sheltered areas, down through the upper pine forest into the mixed pine-oak forests. The dominant alkaloid produced is sparteine, with only traces of minor alkaloids. Nowacki's (1963) contention that sparteine is the primitive alkaloid would suggest that this may be one of the older, more primitive species of *Lupinus* in North America. The trait of many leaflets and the fistulose stems have caused many botanists to mistake this taxon for *L. polyphyllus* which ranges from California and Oregon north into British Columbia. The huge sheathing stipules, however, make *L. montanus* easily recognizable. While *L. polyphyllus* is considered as one of the older taxa of the West Coast, it has the necessary genes to convert or utilize sparteine, changing it into several other alkaloids. The two northern subspecies of *L. montanus* have also modified genomes so that they concentrate other alkaloids. The presence of what appears to be a distinct nectary at the base of the ventral sulcus of the banner and the thickened glandlike upper surface of the base of the staminal tube seem to be unique in *Lupinus*.

While the original description of *L. montanus* failed to mention the sheathing stipules, they are clearly recognizable in the microfiche of the type specimen, and the material from Mt. Orizaba differs from that of Nevada de Toluca only in the hair type being hispidulous to canescent, hence the contention that *L. vaginatus* is a synonym. The type description of *L. flabellaris* clearly mentions the sheathing stipules and topotype material is indistinguishable from the Mexican portion of the taxon, both morphologically and chromatographically.

GUATEMALA. DEP. CHIMALTENANGO: Chichavac, *Skutch 107*(US). Chichoy Pros, *Hunnewell 17145*(GH). San Marcos, *I. R. Johnston 1229*(F). Sierra San Elna, *Siler 2303*(GH). Volcán Acatenango, *Beaman 3258*(GH, MSC, TEX, US); *Standley 61902*(F). Volcán de Agua, *I. R. Johnston 578*(F). Volcán Fuego, N side, *Beaman 4025*(GH, MSC, US). DEP. HUEHUETENANGO: Cumbre Papal, *Steyermark 50945*(F). Between Tocquia and San Juan Ixcoy, *Moncure* in 1950 (F). Between Tunima and Quisil, *Steyermark 48426*(F). DEP. QUEZALTENANGO: Canton La Eseranza Forest, 6 km from San Juan Ostuncalo, *Molina et al. 16648* (F, US). Cerro Lieteoreya, *Koninck 302*(US). 10 mi W of Quezaltenango, *King 3199* (MICH, TEX, US). 11 mi SE of San Marcos, *King 3173*(MICH, TEX, US). Sierra Madre Mts., *Williams et al. 22780*(F, US, WIS), *22800*(F). Volcán Santa María, *Skutch 855*(F, GH, US); *Steyermark 34168*(F). Volcán Santo Tomás, *Steyermark 34857*(F). DEP. SACATEPÉQUEZ: Volcán Agua, *Harmon 3598*(UMO, US, WIS), *3646*(CAS, CUN, F, MICH, MO, UC, UMO, US); *Beaman 2942*(GH, MSC, TEX, US); *Kellerman 4708*(US); *Maxon & Hay 3687* (US); *Molina 21029*(F); *Salas* in Jan. 1926(US); *Shannon 3679*(US); *J. D. Smith 2152* (US); *Standley 65093*(F). DEP. SAN MARCOS: Cerro El Bonito, *Plowman 5044*(GH). Between San Sebastian and summit, *Steyermark 35553*(F); summit, *Steyermark 35530*(F). 2 mi S of San Sebastian, *Williams et al. 25915*(F, WIS). Volcán Tacaná, *Beaman 3230*(GH, MSC, TEX, US); *Steyermark 36140*(F). Volcán Tajumulco, *Beaman 3140*(GH, MSC, TEX, US); *Reeder* in Apr. 1952(MICH); *Shannon 568*(US); *Williams et al. 26996*(F, GH, US). DEP. SOLOLA: Volcán Atitlán, *Beaman 4094*(GH, MSC); *Kellerman 5769*(US); *Steyermark 47508*(F, US). Volcán Santa Clara, *Steyermark 46988*(F). Volcán Tolimán, *Steyermark 47535*(F). DEP. TOTONICAPÁN: Cerro María Tecúm, *Williams et al. 23145*(F). Boundary of Depts. Huehuetenango and Quezaltenango, *Williams et al. 22707*(F, GH, US, WIS). Los

Encuentros y María Tecúm, *Molina 15879*(F, US, WIS). 8 km S of Totonicapán, *Williams et al. 22941*(F, US); *Lind 11*(V, WIS).

MEXICO. CHIAPAS: Mt. Pasitár, *Matuda 70*(MICH, NY, US); *Matuda S-209*(MICH). Volcán Tacaná, *Matuda 2333*(GH, MICH, WIS). COLIMA: Cuchilla, Nevada de Colima, *Goldsmith 57*(F, GH, MO, US). DISTRITO FEDERAL: Cerro Ajusco, *Beaman 2796*(GH, MSC, US); *Garcia* in May 1954(IPN). Pedregal de San Angel, *Barclay & Paxton 530*(F, TEX). Peña de los Charros, *Russell & Souviron 139*(US). GUERRERO: Mina, Cerro Teotepec, *Hinton 14266*(GH, MICH, US); *Rzedowski 16493*(ENCB, MICH). HIDALGO: Plains of Actopan, *Graham 168*(GH). Cerro de las Venturas, N of Pachuca, *Galvan* in Aug. 1963 (ENCB); *Nuñez 56*(UMO). El Chico, *Dunn et al. 20298*(UMO, US). Sierra de Pachuca, *Rose & Hay 5628*(US); *Pringle 9530*(F, GH, MO, US, VT). JALISCO: Nevada de Colima, *Beaman 2366* (MICH, MSC, US); *Matuda 38369*(MEX, UMO); *McVaugh 10076*(MICH, small flowers). MEXICO: 10 km E of Amecameca, *Quijana 51*(ENCB). 11 mi E of Amemeca, *Dodds 11* (MICH); *Montgomery & Root 8114a*(MSC). Cerro Jocotitlán, *Matuda 38490*(MEX, UMO). Crucero?Agua-Blanca, *Hinton 8244*(GH), *8317*(GH, MO, RSA, UMO, US). Crucero-Raices, *Hinton 9031*(F, GH, ENCB, MO, RSA, UMO, US). Estacca, *Matuda 38503*(MEX, UMO). Ixtachuatl, Falda, *Matuda 26148*(NY, US); *Beaman 3477*(GH, MSC, US, $n = 24$); *Nelson & Goldman* in Jan. 1894(US); *Purpus 32*(US), *203*(MO); *Rudd 1029*(UMO, US); *Rzedowski 19806*(ENCB, UMO). Mesón Viejo, *Matuda 38395*(MEX, UMO. Nevada de Toluca, *Balls 4088*(US); *Dunn 18837*(UMO), *18840*(ENCB, MSC, MO, NY, TENN, UMO, US); *Dziekanowski et al. 1915*(MEMO, MO, NY, UC, UMO, WUP), *1932*(ASU, GH, MO, MSC, OSC, SLP, TENN, UMO), *1936*(MEMO, MO, RSA, UMO, US, WUP); *Gallian & Leake 897* (UMO); *Galliotti 3360*(P); *Hunnewell 13146*(GH); *Islas 28*(MEMO); *Mick & Roe 187* (ENCB); *Morales-Diaz* in Aug. 1962(ENCB); *Rose & Painter 7906*(US); *Rzedowski 15782* (ENCB); *Schery 90*(MICH, MO, US). Paso de Cortez, *Iltis et al. 1025*(MICH, MSC, TEX, WIS). Pesco Inst. de Nacional, *Dunn et al. 20373*(F, GA, K, ENCB, MEMO, MO, NEL, NY, ORE, RSA, UC, UMO, US, WUP). Río Frio, *Contreras* in July 1962(ENCB). Tlamacas, vic. of Popocatepetl, *Fonseca F5*(ENCB); *Galicia* in July 1962(ENCB); *Garcia 3A*(ENCB); *Lundell 12358*(MICH, TEX); *Madrigal* in Dec. 1959(ENCB); *Matuda 38497*(MEX, UMO); *Moore 36*(GH); *Quijano 51*(ENCB). Volcán Popocatepetl, *Balls 4227*(US); *Barkley et al.* 2353(TEX); *Beaman 2022*(MSC); *Dunn 18566*(UMO); *18579*(CUN, ENCB, MO, NY, UMO, US); *Galliotti 3368*(P); *Hatheway 1193*(GH, MO, US); *Huerta 101*(ENCB); *Leake & Gallian 133, 141*(UMO); *Lundell 12358*(US); *Rose & Hay 6012*(US); *Ross 8*(US); *Straw & Gregory 1003*(GH, MICH, RSA). MICHOACÁN: Cerro San Andres, 12 km N of Hidalgo, *Beaman 4295*(GH, MSC, TEX, US). Mt. Tancitaro, *Hinton 15593*(US); *Leavenworth & Hoogstraal 1128*(F, MO). Zitácuaro-Cacique Peak, *Hinkson 11932*(US). OAXACA: Atepec, Llano de las Flores, *MacDougal 378.S*(NY). Cerro de San Felipe, *Camp 2869*(NY). Cerro Zemoaltepetl, *Hallberg 790*(ENCB, MICH, US). Cumbre de Sierra de Juárez, *Matuda 38415*(MEX, UMO). Gueletago, *Vilas 31*(WIS). 27 mi N of Ixtlán, Sierra Juárez, *Roe & Roe 1941*(ENCB, MICH, WIS). Macuiltianguis, *MacDougal* in 1960(US). Mt. Zemoaltepec, summit, *E. Nelson 619*(US). Reyes, *E. Nelson 1736*(MICH, US). Sierra de Ixtlán, *Gentry et al. 20272*(UMO). Sierra Madre del Sur, 60 mi NE of Oaxaca, *Webster 11543*(MO). Sierra de San Felipe, *Camp 2869*(NY); *E. Nelson 1135*(US); *Pringle 4779*(F, GH, ISC, MICH, MSC, ND-G, P, US, VT); *C. L. Smith* 333(MO). PUEBLA: Iztaccihuatl, *Beaman 2007*(GH, MSC, US); *Iltis et al. 1025*(TEX); *Weber 372*(ENCB). Pass between Mexico City and Puebla, *Mexia 2647*(MICH), *2647A*(CAS). Alberque Piedra Grande, *Beaman 3640*(GH, MSC, TEX. Ciudad Serdán, *Beaman 2498*(GH, MSC). Pico de Orizaba, *Gelliotti 3343*(P); *Greenman 28*(F); *Liebman 4892*(F, GH), *4893*(F); *Pringle 9528*(F, GH, MO, US, VT); *Schiede 666*(HAL; photos, GH, TEX, UMO, US); *Seaton 510*(GH). Popocatepetl, *Barkley 17Mo87*(F); *Barkley et al. 2353*; *Beaman 1747, 2109*(GH, MSC); *Dunn 18558*(UMO), *18564*(CUN, ENCB, MO, NY, UMO, US); *Miranda & Barkley 17Mo87*(TEX, MSC). TLAXCALA: Mt. Malinche, *Balls 4890*(US). VERACRUZ: Cerro de Perote, *Balls 4604*(US). Cueva

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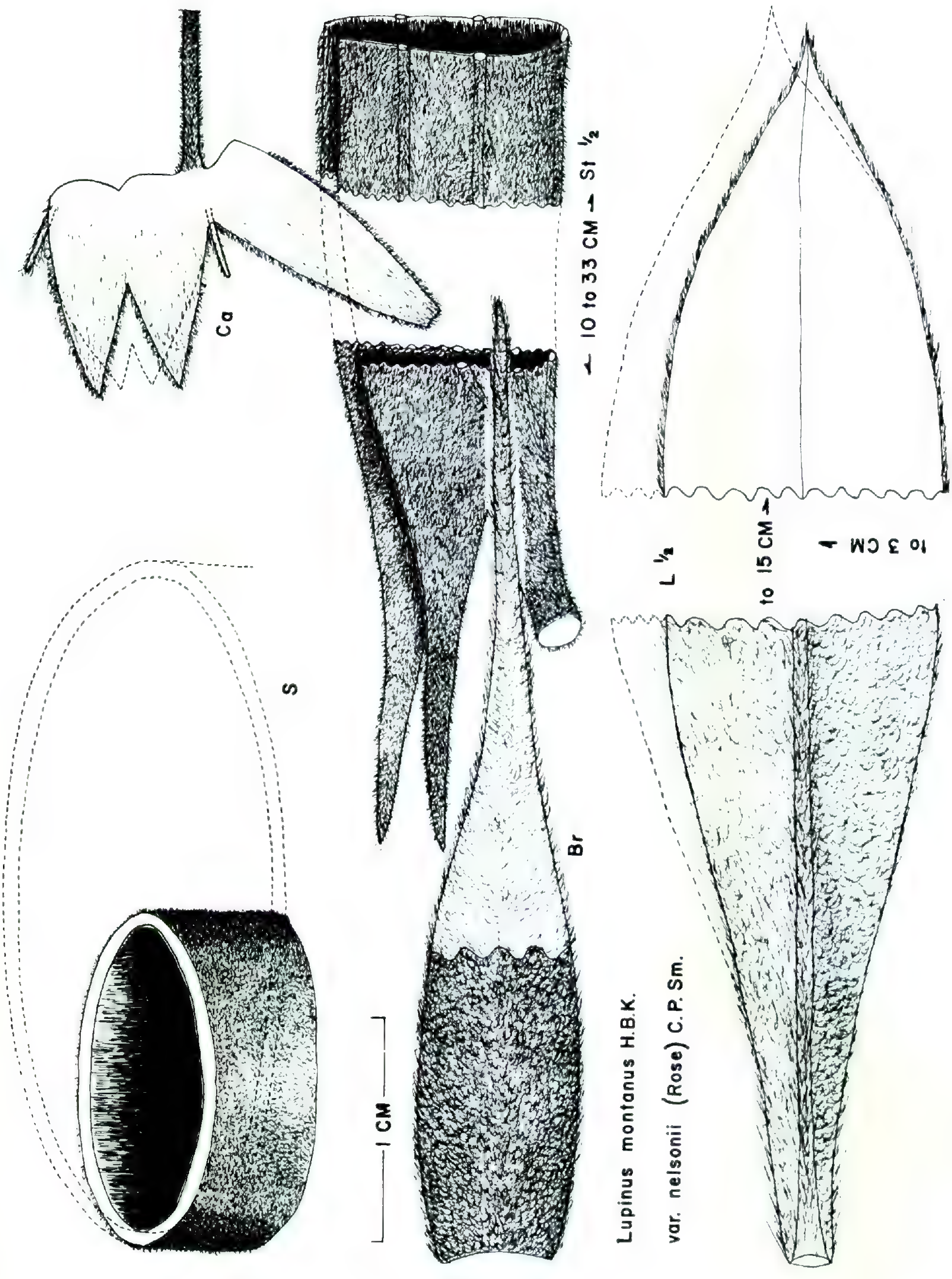
FIGURE 3. Structures of *Lupinus montanus* subsp. *montanus* var. *nelsonii* drawn to mean values, for those traits which differ from var. *montanus*. The calyx, bract and stem are drawn to the scale shown, while the stipule and leaflet are half scale. The lettering is Br = bract; Ca = calyx, inside view; L = leaflet; S = stem; St = stipules. (See legend for Fig. 2 for full explanation.)


Ca
10 to 33 CM
St 1/2
L 1/2
to 15 CM
to 3 CM
S
Br
1 CM
Lupinus montanus H.B.K.
var. nelsonii (Rose) C.P. Sm.

de Muerto, *Beaman 1783*(MSC, US). Pico de Orizaba, *Beaman 2291*(MSC); *E. Nelson 266* (US); *Rose & Hay 5727*(US); *J. G. Smith 391*(MO). Unknown locality, *E. Nelson 38*(US).

1b. **Lupinus montanus** subsp. **montanus** var. **nelsonii** (Rose) C. P. Smith, Sp. Lup. 79. 1938.—Fig. 3.

L. nelsonii Rose, Contr. U.S. Natl. Herb. 8:308. 1905. TYPE: Mexico, Oaxaca, near Cerro de San Felipe, *E. W. Nelson 1145*(US, holotype, photo, UMO).

Differs from *L. montanus* in the large fistulose stems, up to 3 cm or more in diameter, the fistulose nature extending throughout the above ground portion to the top of the raceme; plants to 2.5 m tall; stems densely hispidulous to retrorsely hispidulous; petioles to 50 cm long; leaflets 15, to 15 cm long and 3 cm wide, pilose to canescent below and glabrous above; stipules 10–33 cm long, connate to the petioles for all but 1–2 cm at the tip, the free tips slender attenuate-caudate, both stipules and bracts hispidulous-canescent within as well as densely so without; bracts numerous, plumed, the tips elongate-caudate, 3–4.5 cm long, pilose-canescent, as also the under side of the leaflets, the bracts hiding 5–8 cm of the buds at the tips of the racemes, often subpersistent; flowers the same as the species; pods and seeds the same as the species except the pods densely hispidulous.

The taxon appears to be a gigas form and may represent an ecological modification since there are many typical specimens of *L. montanus* in the region. There are distinctive traits, however, which appear to have a genetic basis, and the taxon has been collected on several occasions from 1894 to 1964. It is also chromatographically similar in its alkaloids to other samples of *L. montanus*.

Mexico. OAXACA: Ixtlán, Atepec, Llanos de las Flores, *MacDougal 378s*(NY). Oaxaca-Tuxtepec Hwy., Llanos de las Flores, *MacDougal* in 1960 (US, 4 sheets). Cerro de San Felipe, *E. Nelson 1145*(US); *Pringle 5839*(GH, VT). Cerro Zemoaltepetl, *Schultes 502*(GH); *Hallberg 790*(MICH, in part). Ixtlán de Juárez, Sierra Ixtlán, *Gentry 20272*(UMO, US). 13 mi N of Ixtlán, *Anderson 4842*(MICH).

1c. **Lupinus montanus** subsp. **montanus** var. **austrovolcanicus** C. P. Smith, Sp. Lup. 90. 1938. TYPE: Guatemala, Volcán Santa María, 8,000–11,500 ft, *E. Nelson 3709*(US-250873, holotype; F, GH, isotypes).—Fig. 8.

Plants perennial, over 3 dm tall; stems hollow, ligneous, 4 mm in diameter, finely appressed puberulent; petioles 6–10 cm long; larger stipules 3–4.5 cm long, wide, membranous, sparsely pilose to canescent inside and outside, the free tips 7–11 mm long; leaflets 10–11, linear, acute, mucronate, the longest 5.5–6.5 cm long, 6–8 mm wide, sparsely strigose above, thinly kinky canescent beneath; peduncles 2–8 cm long; racemes ca. 8 cm long, verticillate, the lower whorls to 2 cm distant; bracts ca. 16 mm long below; pedicels 5–6 mm long, slender sericeous-puberulent; calyces canescent without, finely sericeous within near the tips of the lips, the lower lip slender, arcuate, 8–9 mm long, entire, the upper lip ovate, bidentate, 7 mm long, the lips connate laterally 2 mm, the bracteoles 1.5–2 mm long, attached near the lip of the lateral sinuses; banner suborbicular, glabrous or occasionally sparsely hairy on the distal portion of the dorsal crest, 11.5–12 mm long, 11–11.5 mm wide, widest above the midpoint, reflexed 6.7 mm, appressed 7 mm; wings 12.8–13 mm long, 7 mm wide; keel

with minute papillae above the claws, 3.5 mm wide in the middle, the angle 95°–100° at anthesis; ovules 6–7; pods 3–4.5 cm long, 9 mm wide, pilose with hairs 1–2 mm long.

The specimens seen appear to represent hybridization and introgression from *L. kellermannii.* The slender woody stems, short stature of the plants, narrow smaller leaflets, intermediate petioles, and the presence of pubescence dorsally on the banners of about half of the specimens all suggest introgression. The flower size and stipules are distinctly like those of *L. montanus.*

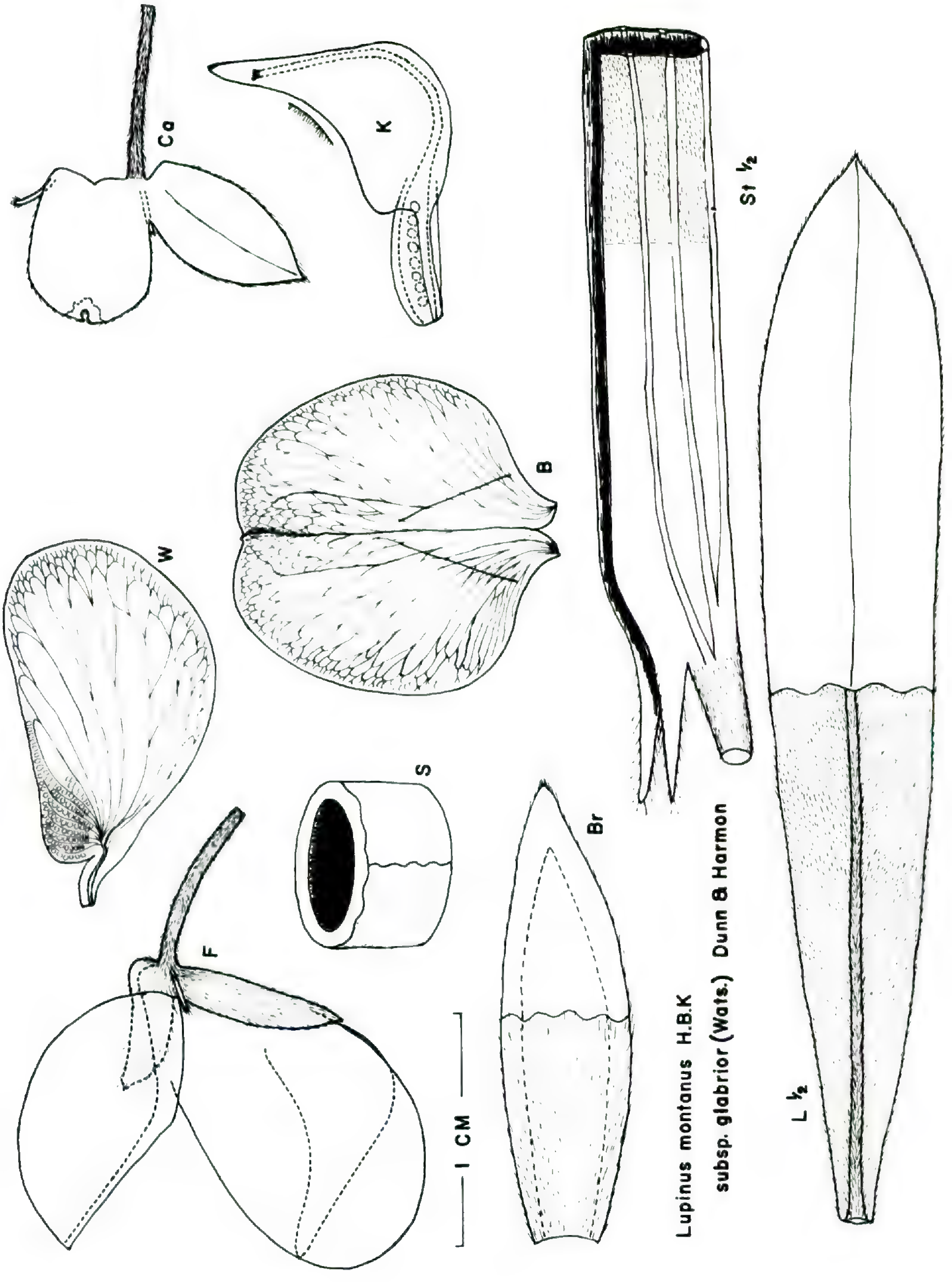
GUATEMALA. DEP. QUEZALTENANGO: Volcán Santa María, *Beaman 4124*(ENCB, MSC, TEX, US); *E. Nelson 3709*(F, GH, US); *Steyermark 34205*(F). Above Palojunoj, *Standley 67703, 67707, 67738*(F), *67683*(F, intermediate to var. *montanus*).

1d. **Lupinus montanus** subsp. **glabrior** (Wats.) Dunn & Harmon, comb. nov. —FIG. 4.

L. montanus var. *glabrior* Wats., Proc. Amer. Acad. Arts 23:270. 1888. TYPE: Mexico, Chihuahua, summit of Sierra Madre, *Pringle 1206*(GH, holotype; F, G, K, ND-G, P, RSA, US, VT, isotypes; photo, UMO).
L. glabrior (Wats.) Rose, Contr. U.S. Natl. Herb. 8:308. 1905.

Plants perennial, to 1 m tall; stems glabrous to glabrate, ligneous ridged, at least on drying, fistulose, 6–8 mm in diameter; petioles 12–20 cm long, the free portion finely strigose; stipules membranous, sheathing and often imbricate on dwarfed branches, 4.5–6 cm long, the free tips only 3–6 mm long; leaflets 14–15, the largest 9–11 cm long, 12–13 mm wide with acute-mucronate tips, glabrous above, sparsely and finely puberulent below; peduncles to 17 cm long; racemes 20–30 cm long at maturity, verticillate, the lower whorls, 2.5–3 cm distant, the rachis finely but densely puberulent; bracts broadly lanceolate, membranous, gradated, the lower to 2 cm long, the upper reduced, minutely puberulent without, glabrous within; pedicels 6–8 mm long; calyces with broad boat-shaped lips, finely puberulent without, glabrous within, the lower lip 7–8 mm long, entire, the upper lip 5–7 mm long, the apex blunt with an irregular notch 0.5–0.8 mm deep, the lips connate 1.4 mm, the bracteoles straplike, 2–3 mm long, glabrous, except for a few setaceous hairs near the tips; corollas glabrous except for a few papillae above near the claws of the keel or occasionally the keel ciliate above toward the acumen; banner orbicular, 13–14 mm long, 13–15 mm wide, reflexed 7 mm, appressed 6.5–6.8 mm, the sulcus 2.4 mm deep midway between the umbo and the base, the banner angle 133°–150°; wings 15–17 mm long, 8–10 mm wide; keel 4–5.3 mm wide in the middle, the angle 80°–85°, occasionally papillae near the claws or occasionally ciliate above near the acumen; ovules 7–9; pods 8–8.5 mm wide, 3.5–4.5 cm long, thinly strigose; seeds nearly black with mottling, 4.5 mm long, 3 mm wide, a pit at the funicular attachment.

The subspecies *glabrior* is known only from northern Durango and Chihuahua, from the summit of the Sierra Madre Occidental, in rather inaccessible areas. The area is north of that of subsp. *montesii* and subsp. *montanus*, as well as the fact that there are distinctive morphological traits in addition to distinct



Lupinus montanus H.B.K
subsp. glabrior (Wats.) Dunn & Harmon

chromatographic differences. The best distinguishing traits are the short, blunt upper lip of the calyx and the lanceolate bracts. While other traits are distinct, they are not as easily recognized. Since the geography, ecology, morphology, and chromatography suggest a distinct gene pool, subspecific rank is suggested. The large stipules and the floral morphology clearly indicate the affinity to *L. montanus.*

MEXICO. CHIHUAHUA: Vic. of Chuchuichupa, summit of Sierra Madre, *Pringle 1206*(GH, F, G, K, ND-G, P, RSA, US), *1579*(P). Cerro Mohinora, 10 mi S of Guadelupe y Calvo, *Straw & Foreman 1943*(ENCB, MICH). DURANGO: Sierra Madre, 30 mi N of Guanaceví, *E. Nelson 4785*(US).

1e. **Lupinus montanus** subsp. **montesii** (C. P. Smith) Dunn & Harmon, comb nov.

L. montesii C. P. Smith, Sp. Lup. 41. 1938. TYPE: Mexico, Sinaloa, Cerro de San Rafael, San Ignacio, *Montes & Salazar 112*(US, holotype).—FIG. 5.

Plants perennial, from a woody caudex, 4–7 dm tall; stems hollow, glabrous below, sparsely strigose on the peduncle, rachis of raceme, and petioles, ligneous ridged, at least on drying, 6–8 mm in diameter; longest petioles 10–19 cm long, strigose on the portion not fused to the stipules; stipules sheathing and encircling ¾ of the stem, 4–10 cm long, the free, caudate tips 1–2 cm long, glabrous except for a few scattered setae near the tips; leaflets 9–14, linear-elliptic to narrowly elliptic, glabrous above, sparsely strigose below, the largest 6.5–9 cm long, 6–12 mm wide, acute-mucronate at the tips; peduncles hollow, 7–14 cm long, sparsely strigose; racemes verticillate to subverticillate, 20–35 cm long, rarely only 7 cm long in depauperate specimens, the rachis more densely strigose; bracts membranous, the long caudate tips with scattered setaceous hairs, caducous, 1.0–3.5 cm long, broad and completely covering the flower buds at the tip of the raceme, pedicels filamentous, 5–8.8 mm long, densely strigose; calyces appressed puberulent outside, glabrous within, the lower lip 8–12 mm long, generally entire, occasionally with a notch 0.1 mm deep, the upper lip 6–9.5 mm long, with an apical notch 0.3–1.6 mm deep, the base gibbous above, the lips connate 1.2–2 mm, a glabrous spatulate bracteole 1–4 mm long attached near the lip of the lateral sinuses; corollas blue and white, glabrous but the keel sometimes ciliate; banner 11.6–15.9 mm long, 12.5–17.4 mm wide, reflexed 6.4–7.7 mm, appressed 5.5–7.4 mm, reflexed/appressed ratio (average 1.17), banner angle 130°–149° (average 141°); wings 13–18.4 mm long, 8.4–10.4 mm wide, the claw on the average 3.2 mm long; keel 3.8–5.2 mm wide in the middle, the angle 89°–98° (average 91°), ciliate above near the acumen in half of the specimens, the others glabrous; ovules 10–13; only immature legumes seen, these strigose.

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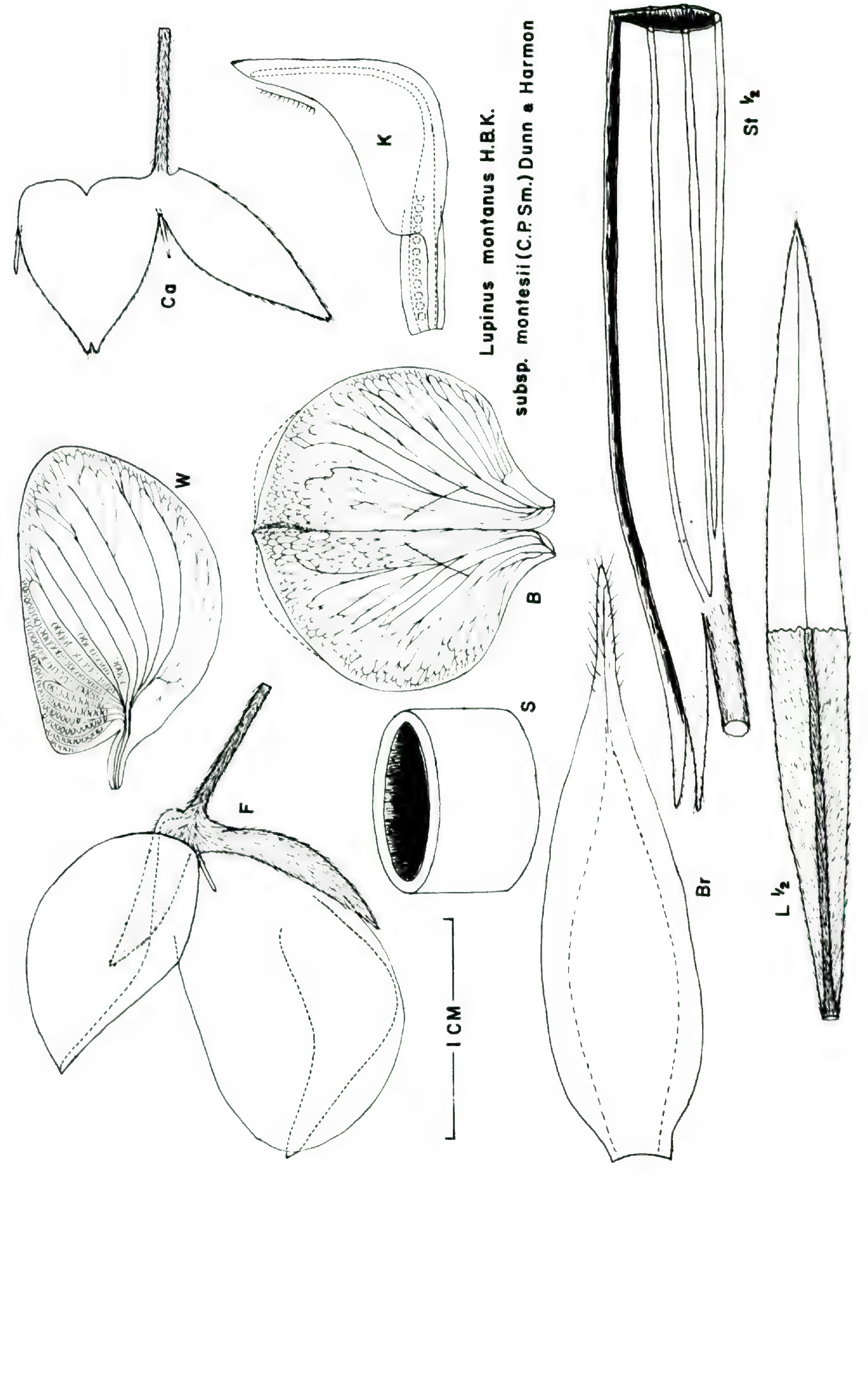
FIGURE 4. Structures of *Lupinus montanus* subsp. *glabrior* drawn to mean values, for the differences from subsp. *montanus*. All parts are drawn to the scale shown except the stipules and the leaflet which are drawn to half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)



Lupinus montanus H.B.K. subsp. montesii (C.P. Sm.) Dunn & Harmon

The subspecies is known only from southwestern Durango, Mexico, in the general area of El Salto, and from Cerro de San Rafael, Sinaloa. Most of the collections have been west of El Salto but some have been cited as 45 miles to the south. The elevations have been near 7,000 ft, which is well below the normal altitude for *L. montanus*. The distribution is also geographically distinct from that of the species. Since the ecology, geography, morphology, and the composition of the alkaloids, are distinctive, it is suggested that there is a sufficiently distinct gene pool to recognize the taxon at the subspecific level. It is also distinct from subspecies *glabrior* in geography, morphology, and in chromatography. The large sheathing stipules and the floral morphology leave no doubt as to its affinity with *L. montanus*.

MEXICO. DURANGO: Cerro Auehueto, S of Huachicheles, *Maysvilles 7258*(MICH). Between Durango and Mazatlán, *Pennington 242, 243*(TEX). El Salto, *Guzman* in Sep. 1961 (ENCB). 20 km S of El Salto, *Gordon 41*(MICH, × *L. madrensis*). 19 mi SW of El Salto, *Waterfall 15490*(OKLA). 33 mi SW of El Salto, *Waterfall 12714*(OKLA, UMO). 3 mi W of La Ciudad, *LeDoux et al. 2024*(C, CAS, G, ENCB, K, MEX, MO, NY, U, UC, UMO, US). 6 mi W of La Ciudad, *Flyr 274*(TEX). 13 mi E of La Ciudad, *LeDoux et al. 1996*(ENCB, MEX, MO, NY, UMO, US). 8.4 mi W of La Ciudad, *Reveal & Atwood 3507*(MARY, UMO); *Breedlove 18877*(CAS, UMO). 14.3 mi NE of La Ciudad, *Pinkava et al. 9495*(ASU, UMO). 54 mi N of Estación Coyotes, *Breedlove 18789*(CAS, ENCB, UMO). Metates, N of Cueva, *Pennell 18408*(GH, US). Road to Pueblo Nuevo, *Maysvilles 7760*(MICH, × *L. madrensis*). W of Pueblo Nuevo, *Maysvilles 8071*(MICH, TEX). SINALOA: Cerro de San Rafael, San Ignacio, *Montes & Salazar 112*(US).

2. **Lupinus cacuminus** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 79. 1940. TYPE: Mexico, Nuevo León, peak of Cerro Potosí, Municipio de Galeana, *Mueller 2269* (F, holotype; GH, MO, isotypes) [*Mueller 1257* (F) labeled type in Standley's handwriting].—FIG. 6.

Plants perennial, caespitose, 3.5–6 dm tall; stems from a caudex, fistulose, the internodes between fully developed leaves only 1–3.5 cm long, pubescence all appressed-sericeous but of multiple hair types and lengths, the upper 2 or 3 nodes with branches initiated by anthesis of the primary racemes; largest petioles 5.5–13 cm long, reduced progressively upward, persistent long after the leaflets drop; stipules gradated from 4.5 cm long below to 1.5 cm above, imbricated below, connate 3 cm below to only 7–8 mm above, the free tips subulate-caudate; leaflets 10–14, linear-elliptic, appressed silky villous on both sides, sparsely above and the central area often glabrous, the largest 3–4 cm long, 3–4 mm wide (to 6 mm wide in a population on Peña Nevada), the tips acute and mucronate; peduncles 4–5 cm long, exceeded by the foliage; racemes 10–13 cm long but numerous bracts in a terminal tuft suggest that they may get much longer, the flowers tightly and spirally arranged; bracts lance-subulate, tardily deciduous or semipersistent; pedicels 6.5–12 mm long, hispidulous; calyces silky

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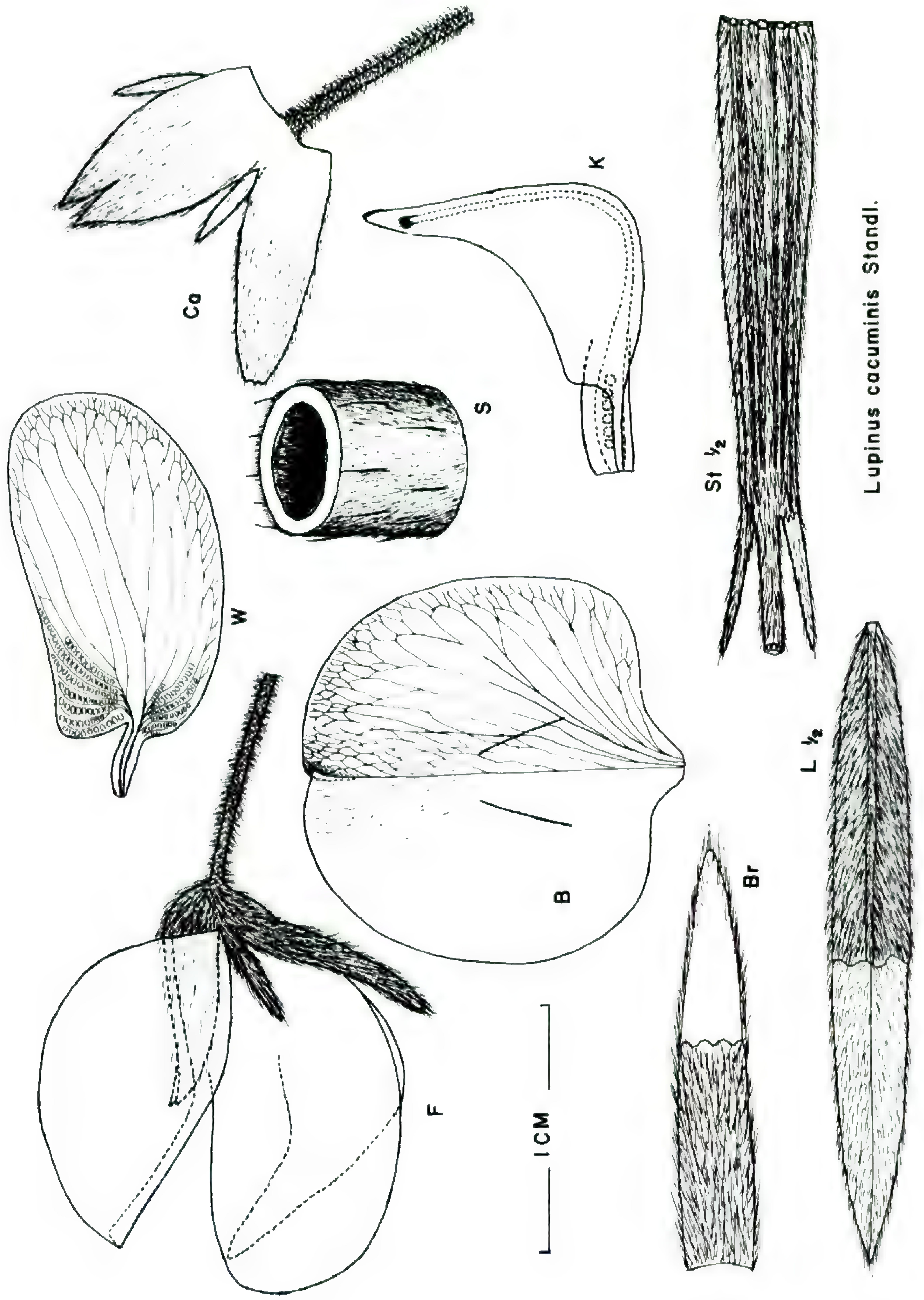
FIGURE 5. Structures of *Lupinus montanus* subsp. *montesii* drawn to mean values, for the differences from subsp. *montanus*. All parts are drawn to the scale shown except those for the stipules and leaflet, which are drawn at half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)


Ca
K
S
W
B
F
1 CM
St ½
L ½
Br
Lupinus cacuminis Standl.

white-villous with appressed hairs, the lower lip oblong-lanceolate, 8–10.2 mm long, tridentate or entire, the teeth 0.2–0.4 mm deep, the upper lip 7.7–10.4 mm long, bifid, the notch 1–4 mm deep, the lip oblong, 3.5–4 mm wide, flattened, the lips connate 1.4–2 mm, the bracteoles lanceolate, 1.5–6 mm long, attached at the lip of the lateral sinuses; banner sparsely pubescent dorsally on the distal portion, the tip emarginate, 14–17.5 mm long, 13–17.6 mm wide, reflexed 7–10 mm, appressed 6–8.5 mm, the angle 140°–155°, the sulcus 1.5–1.8 mm deep midway; wings 15–17.4 mm long, 7–9.5 mm wide, the claw 2.5–3 mm long; keel 4–5 mm wide in the middle, glabrous or ciliate above near the acumen, the angle 80°–90° at anthesis; ovules 5–7; pods 4–5 cm long, 9–11 mm wide, densely lanate with hairs 2 mm long.

While collectors have reported the plants as abundant in the upper pine woods and above timber line on Cerro Potosí, they have only been collected on three mountain peaks: Los Alpes, Cerro Potosí, and Peña Nevada. Flowering occurs from June through July and as late as August. The taxon appear intermediate between *L. montanus* and *L. muelleri* in several characteristics but has essentially the same spectrum of alkaloids as *L. montanus*. The specimens from Peña Nevada have sparse ciliation near the acumen of the keel.

MEXICO. COAHUILA: Los Alpes, 40 mi E of Saltillo, *Gentry et al. 20059*(UMO, US). NUEVO LEÓN: Cerro Potosí, Municipio de Galeana, *Mueller 2269*(F, GH, MICH, MO). Biol. Exp., U. of Ill., *Schneider 958*(F, GH, MICH, MO). Cerro Potosí, top of mt., *Beaman 2654* (GH, MSC, US); *Gilbert 26, 29*(TEX); *Hinton 17038*(MICH). Cerro Potosí, near microwave tower, *Dunn et al. 20203*(F, K, MO, NY, RSA, UC, UMO, US); *Dziekanowski et al. 1761*(GH, ENCB, K, MEMO, MEX, MICH, MO, MSC, UMO, WUP); *MacGregor et al. 314*(KANU, UMO). 20 mi E of Galeana, *Mueller 1257*(F, GH, MICH, TEX). Peña Nevada, 26 mi NE of Dr. Arroyo, top of Picachio Onófre, *Beaman 2690*(GH, MSC, US). TAMAULIPAS: Peña Nevada, E and S slopes, *Stanford et al. 2597*(DAO, U, US). Summit of Peña Nevada, *G. Gillett 1237*(MSC).

3. **Lupinus muelleri** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 80. 1940. TYPE: Mexico, Nuevo León, Las Canoas, on Cerro Potosí, Municipio de Galeana, *Mueller 2205* (F, holotype; CAS, GH, MICH, MO, TEX, isotypes).—FIG. 7.

Plants perennial; stems few to many from a woody caudex, woody with a solid pith, erect, 5–7 dm tall, 3 mm in diameter, branching from the upper nodes, thinly appressed strigose, with a cinereous undercoat of kinky hairs 0.2–0.4 mm long; petioles 1–2 cm long, filiform; stipules subulate to filiform, 6–8 mm long, connate to the petioles 2–4 mm; leaflets 6–8, the largest 2–2.5 cm long, elliptic-oblanceolate, the tip acute, mucronate, both surfaces densely strigose; peduncles 2.5–3.5 cm long; racemes 6–10 cm long, the flowers scattered to subverticillate; bracts subulate, 8–8.5 mm long, strigose outside; pedicels 7–11 mm long, with

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FIGURE 6. Structures of *Lupinus cacuminus* drawn to the means values on the scale shown. The stipules and leaflet are drawn to half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)

hispidulous hairs 0.4 mm long; calyces sericeous outside, 2-lipped, the lower lip arcuate, boat shaped, 7.5–9 mm long, 3–4 mm wide, entire, or with teeth 0.2 mm long, the upper lip ovate, 7–7.4 mm long 3.8–4.5 mm wide toward the base, the apical notch 0.1–0.8 mm deep, the lips connate 1.2–1.4 mm, the bracteoles 0.8–2.0 mm long, linear, attached below the lateral sinus lips; banner sparsely pubescent dorsally near the distal portion, suborbicular, widest below the midpoint, reflexed 7.5–8.2 mm, appressed 6–7 mm, the angle 138°–145°, the sulcus 1.5–1.8 mm deep, midway; wings glabrous, obovate, 13–15 mm long, 7–7.9 mm wide; keel ciliate above from the middle toward the acumen, 4–5 mm wide in the middle, the angle 83°–88°; ovules 6–8; pods 4–5 cm long, 10–12 mm wide, thinly subappressed kinky pilose, the hairs to 1 mm long; seeds 6.4 mm long, 5.7 mm wide, tan with faint mottling.

Thus far known only from Coahuila and Cerro Potosí in Nuevo León, where it was reported as abundant in pine woods, at elevations near 3,000 m. Flowering occurs from June to August.

MEXICO. COAHUILA: Puerto de la Siberio, Arteaga, *Marroquin 14*(MEMO). NUEVO LEÓN: Cerro Potosí, Las Canoas, Municipio de Galeana, *Mueller 2205*(CAS, F, GH, MICH, MO, TEX). Above Ejido, *Beaman 3311*(F, GH, ENCB, MSC, TEX); *Dunn et al. 20247*(UMO); *Dziekanowski et al. 1770*(CAS, G, ENCB, MO, NY, ORE, P, RSA, UC, UMO, US), *1771* (GH, ENCB, MEMO, MEX, MO, MSC, NY, RSA, SLP, UC, UMO, US, WUP).

4. **Lupinus kellermanianus** C. P. Smith, Sp. Lup. 90. 1938. TYPE: Guatemala, Volcán Agua, 9,000 ft, *Kellerman 4746* (US, holotype).—FIG. 8.

Plants perennial, shrubby; woody stems solid, the branches sometimes hollow, 3–6 mm in diameter, first year stems only 3 mm in diameter, strigose; petioles filiform, 2–4.5 cm long on the upper branches; stipules 8–18 mm long, the smallest at the base of the branches, the longest above, subulate-attenuate, connate 5–10 mm; leaflets 7–9, lanceolate, the tips acute, mucronate, the largest leaflets 2.5–3.5 cm long, 5 mm wide, sparsely kinky-villous above, canescent to kinky-villous below; peduncles 3 cm long at anthesis, 3–8 cm at fruiting; racemes 3–6 cm long, verticillate; bracts subulate-attenuate, 8–14 mm long, canescent; pedi-

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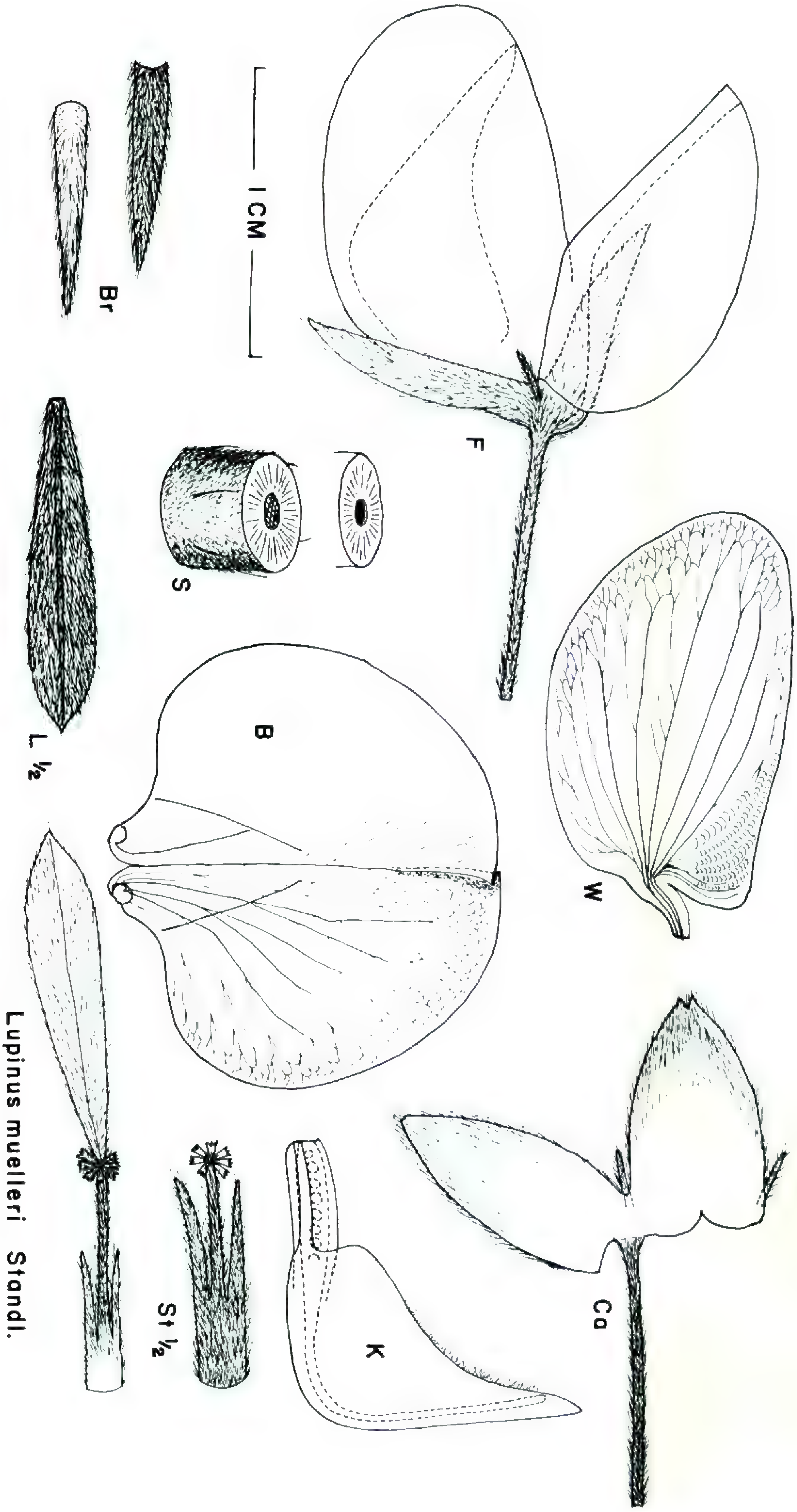
FIGURE 7. Structures of *Lupinus muelleri* drawn to the mean values on the scale shown, except the stipules and leaflet which are half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)

FIGURE 8. The vegetative structures for *Lupinus montanus* subsp. *montanus* var. *austrovolcanicus* are shown in the upper portion for comparison with *L. kellermanianus*. The stipules and leaflet are shown at half the scale. The floral traits are the same as shown for *L. montanus* subsp. *montanus* var. *montanus* in Fig. 2. The lower portions shows the structures of *L. kellermanianus* drawn to the mean values on the scale shown. The stipules and leaflet are drawn to half scale. The lettering is: B = banner, dorsal view; Br = bract; C = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)

FIGURE 9. Structures of *Lupinus valerioi* drawn to the mean values at the scale shown, except the stipules and leaflet which are half scale. The lettering is: B = banner, dorsal view; Br = bract; Ca = calyx, inside view; F = flower, left side view; K = keel; L = leaflet; S = stem; St = stipule; W = wing. (See legend for Fig. 2 for full explanation.)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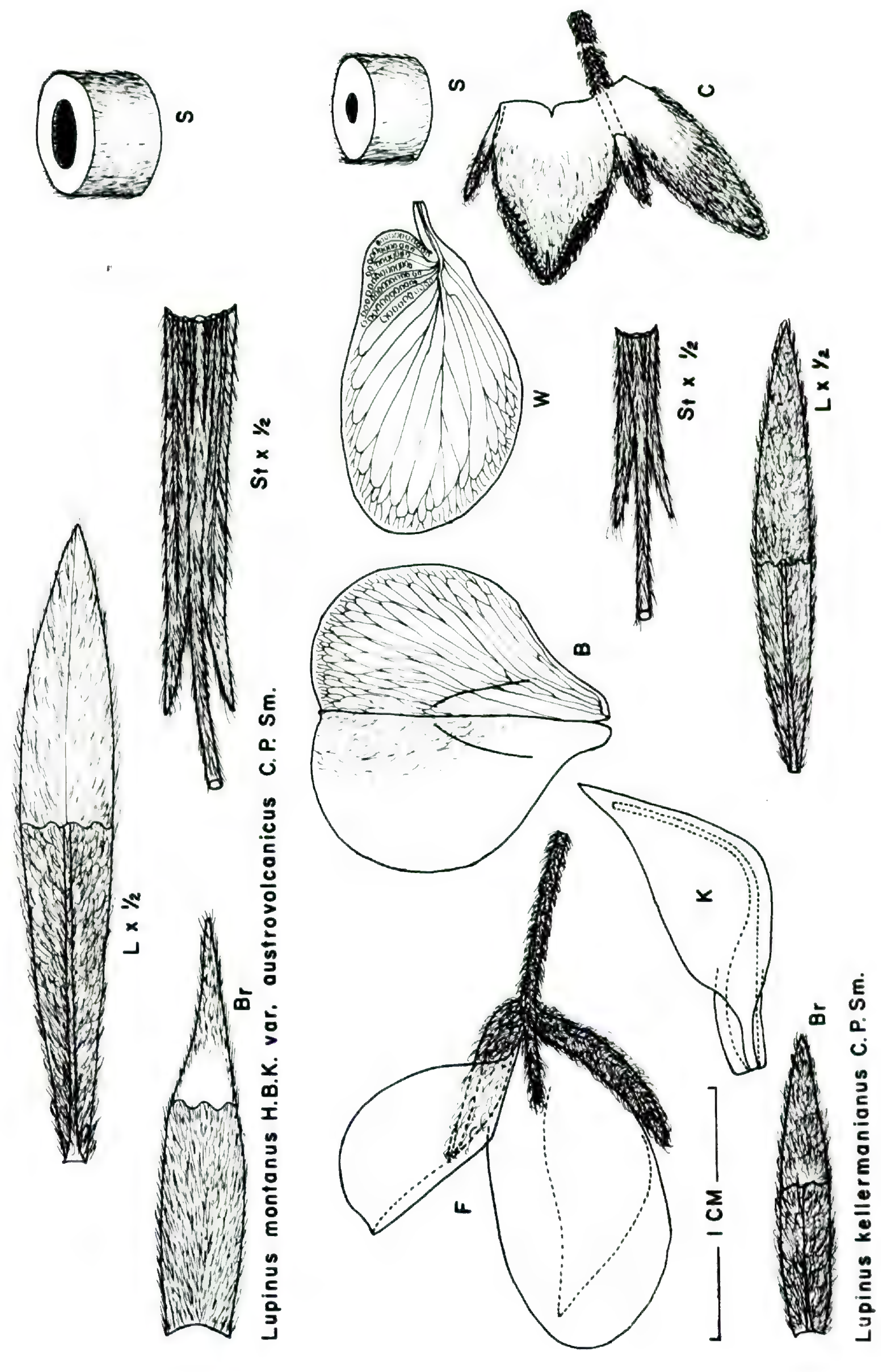
Lupinus muelleri Standl.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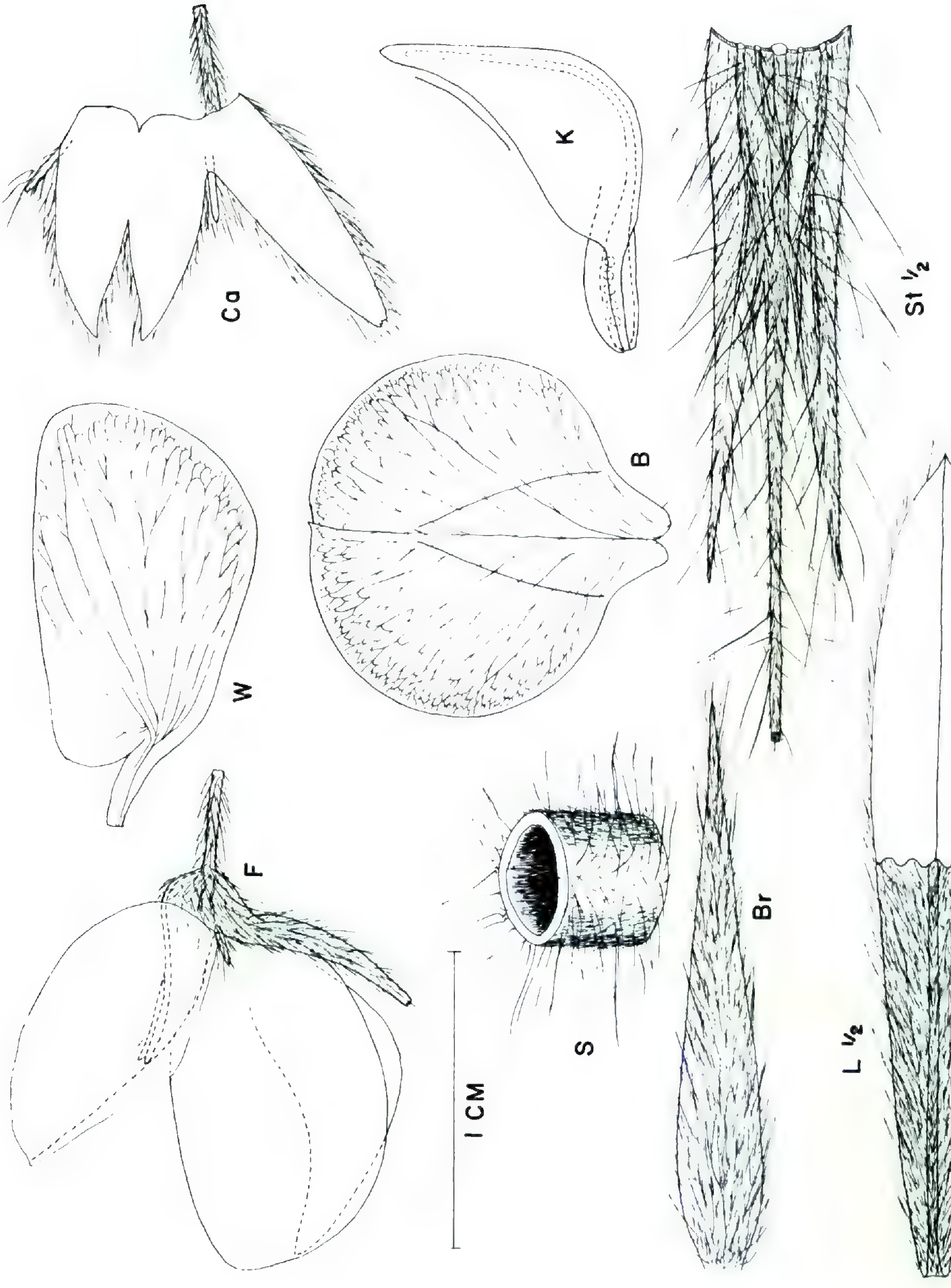
Lupinus kellermanianus C. P. Sm.



Lupinus valerioi Standl.

cels 5 mm long at anthesis, 10–12 mm in fruit, hispidulous; calyces canescent, the lower lip 7.5–8.5 mm long, strigose within on the distal half, the upper lip 6.6–6.8 mm long, the notch 1.2–1.4 mm deep, the lips connate 1.5 mm laterally, the bracteoles lanceolate, 3–4 mm long, attached well below the lateral sinus lip on the side of the calyx cup or at the base; banner with a sparse patch of kinky hairs distally on the dorsal side, densest on the crest, obcordate to suborbicular, 12 mm long, 11.5–12 mm wide, reflexed near the midpoint; wings glabrous, 12–14 mm long; keel glabrous, 4–4.5 mm wide in the middle, the acumen very short; ovules 6–7; pods 3.5 cm long, 7 mm wide, sparsely pilose; seeds not available.

Very few collections have been made of this species known only from Volcán Agua and Zunil. The traits of the woody stems and pubescence on the banner have shown up on several neighboring peaks in plants which are otherwise typical *L. montanus.* This suggests introgression and the material named *L. montanus* var. *austrovolcanicus* is probably of hybrid derivation.

GUATEMALA. QUEZALTENANGO: Summit of Volcán Zunil, *Steyermark 34848*(F). SACATEPÉQUEZ: Volcán Agua, 9,000 ft, *Kellerman 4746*(US); *Kellerman 15*, 1905(US).

5. **Lupinus valerioi** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 545. 1937. TYPE: Costa Rica, San José, Cerro de las Vueltas, *Standley & Valerio 43668* (holotype F).—FIG. 9.

Plants perennial, 6–9 dm tall, woody below; stems of current season hollow, subfistulose, to 5 mm in diameter, with abundant spreading pilose hairs 3–4 mm long, and with an undercoat of appressed strigose hairs; petioles of mature leaves, 6–12 cm long, pubescence as on the stems; stipules 2.5–4.5 cm long, connate to the petioles 1–2.5 cm, pilose, the free portion slender subulate-attenuate; leaflets 7–10, slenderly oblanceolate, the largest 4–7 cm long, 7–10 mm wide, glabrous above, subappressed strigose below; foliage dense from short internodes causing the lower stipules to be imbricated on the branches, 2–3 cm, with multiple leaves from the lateral buds of the upper nodes; peduncles 8–10 cm long; racemes 6–17 cm long, those of the branches shorter, verticillate to subverticillate, the whorls 10–25 mm distant in age; bracts caducous, lance-attenuate, 15–23 mm long, 2–3 mm wide in the lower portion of the raceme, with numerous pilose hairs 2–3 mm long dorsally; pedicels 3–4 mm long at anthesis, spreading pilose, the hairs 1–2 mm long; calyces densely subappressed pilose, the hairs 1–2.5 mm long, the lower lip 8.5–10.6 mm long, the tip bi- or trifid, the teeth 0.1–0.3 mm long, the upper lip 6–8.5 mm long, bifid, the notch 3.5–5.5 mm deep, the lips connate laterally 1.8–2.4 mm, the bracteoles 1.5–2.5 mm long, attached on the calyx cup below the lateral sinuses, with the lower portion fused to the calyx cup; banner glabrous, suborbicular, somewhat constricted below into a broad claw, 12–14 mm long, 11–12.5 mm wide, reflexed 5.5–6.5 mm, appressed 6.5–7 mm, reflexed/appressed ratio 0.76–0.83; wings 13.5–16.5 mm long, 6.5–8 mm wide, the claws 2.8–3.4 mm long; keels generally minutely ciliate above on the distal part, 3.5–4.5 mm wide in the middle, the angle 90°–95°; ovules 5; pods 3–3.5 cm long, 8.5–9.5 mm wide, densely villous, the hairs 2–3 mm long; seeds 4.5 mm long, 3 mm wide, dark brown to black.

The stipules and bracts show derivation from the *L. montanus* genome, which apparently was introduced and introgressed with a local taxon which at the present time appears to have dominated most of the characteristics, with only the vestige of traits from *L. montanus*. The flowering and fruiting materials have been collected from September through January at elevations from 2,700–3,100 m.

COSTA RICA. SAN JOSÉ: Cerro Chirripó, *Evans et al. 118*(MICH). Cerro Frio, *Jiménez 2677*(CR, F). Cerro Vueltas, *Standley & Valerio 43668*(F), *43974*(F, US). Cord. Talamanca, *Weber 6257*(MICH).

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GUAYANIA DAVIDSEI AND *HEBECLINIUM GENTRYI*, NEW SPECIES FROM NORTHERN SOUTH AMERICA (EUPATORIEAE–ASTERACEAE)[1]

ROBERT M. KING[2] AND HAROLD ROBINSON[2]

ABSTRACT

Descriptions and discussions of relationships are provided for *Guayania davidsei* R. M. King & H. Robinson from the Amazonas region of Venezuela and *Hebeclinium gentryi* R. M. King & H. Robinson from the Chocó region of Colombia.

Collecting efforts of two members of the staff of the Missouri Botanical Garden have provided two new species belonging to the *Hebeclinium* complex of the tribe Eupatorieae (King & Robinson, 1971a, 1971b). The complex is notable for the partially deciduous subimbricate involucral bracts, the simple structure of the style base, the smooth corolla lobes, the long nonannulated anther collars, and for a tendency to bear hairs on the receptacle. The latter character which was the traditional distinction of *Hebeclinium* is, however, not consistent throughout the group, being absent in some species of *Hebeclinium* sens. str. and lacking in all species of *Guayania*. The genera *Hebeclinium* and *Guayania* are most easily distinguished by the extremely filiform style appendages of the former and by the strongly asymmetric carpopodium of the latter. With the present additions *Hebeclinium* has 19 species concentrated in the northern Andes with one species, *H. macrophyllum* (L.) DC., widely distributed. *Guayania* now contains 6 species all restricted to the Guayana Highlands region and to the surrounding lowlands of the Orinoco and Amazon.

Guayania davidsei R. M. King & H. Robinson, sp. nov.—FIG. 1.

Plantae herbaceae perennes erectae ca. 4 dm altae pauce ramosae. Caules succulenti anguste jatrophiformes superne abbreviati et in inflorescentia abrupte terminati glabri et in sicco irregulariter striati. Folia opposita superne congesta, petiolis 4–6 cm longis; laminae ovatae 9–12 cm longae et 6.0–7.5 cm latae penninervatae base late obtusae margine serratae apice vix breviter acuminatae supra et subtus glabrae vel ad marginem sparse puberulae. Inflorescentiae laxe cymosae, ramis dense puberulis, pedicellis 0.3–1.5 mm longis. Capitula 5.0–5.5 mm longa et 3–4 mm lata; squamae involucri ca. 28 et 4–5-seriatae 1.0–4.5 mm longae ad 1 mm latae exteriores late ovatae interiores sensim oblongae vel anguste lanceolatae margine et apice distincte scariosae et minute puberulae apice late vel anguste rotundatae extus glabrae et plerumque 3-striatae; receptacula leniter convexa glabra. Flores ca. 22 in capitulo; corollae albae tubulosae ca. 3 mm longae, faucis tubulosis base indistinctis, lobis ca. 0.3 mm longis et 0.25

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ANN. MISSOURI BOT. GARD. 64: 366–370. 1977.

FIGURE 1. *Guayania davidsei* R. M. King & H. Robinson, holotype, United States National Herbarium. Photo by Victor E. Krantz, Staff Photographer, National Museum of Natural History.

mm latis, faucis superioribus et lobis extus breviter puberulis, pilis moniliformibus; filamenta in parte superiore ca. 0.25 mm longa; thecae ca. 0.8 mm longae; appendices antherarum oblongae ca. 0.15 mm longae et latae; grana pollinis ca. 18 mμ in diametro; achaenia 1.5 mm longa plerumque in costis breviter setifera;

setae pappi ca. 25 tenues ca. 3 mm longae superne non latiores, cellulis apicalibus argute acutis.

TYPE: VENEZUELA. AMAZONAS: 20 km S of Puerto Ayacucho, 100 m, low forested hills E of highway with savanna at base, at edge of large boulder outcrops in forest in shade—at least partially—on small hills, heads white, 2 Nov. 1971, *Gerrit Davidse 2845* (US, holotype; MO, isotype).

Guayania davidsei is the second member of the genus with modified stem structure and abrupt bases on the inflorescences. In this species the stems are somewhat thickened with more congested leaves in the upper part, providing the superficial resemblance to a *Jatropha.* The related *G. bulbosa* (Arist.) R. M. King & H. Robinson has stems completely underground and tuberous. The latter species also differs by the glanduliferous branches of the inflorescence. The new species is apparently from low elevations, while *G. bulbosa* is reported from talus slopes at 1,500 m elevation on Serrania Parú.

Hebeclinium gentryi R. M. King & H. Robinson, sp. nov.—FIG. 2.

Plantae suffrutescentes erectae ca. 1 m altae? Caules obscure tetragoni sordide lanosi. Folia opposita, petiolis 0.5–1.0 cm longis; laminae ovatae 3.5–7.0 cm longae et 1.8–3.7 cm latae base breviter obtusae vel subrotundatae margine minute serratae vel duplo-serratae apice distincte breviter acuminatae supra virides glabrae vel glabrescentes fere ad marginem et nervis primariis minute puberulis subtus fulviores obscure glandulo-punctatae in nervis et nervulis dense sordide puberulae, nervis secondariis pinnatis valde ascendentibus paucis. Inflorescentiae corymboso-paniculatae, ramis dense puberulis, ramulis ultimis 1–5 mm longis. Capitula plerumque 5 mm alta et 3.5–4.0 mm lata; squamae involucri ca. 40 subimbricatae 4–5-seriatae valde inaequales 1–3 mm longae 0.3–0.6 mm latae anguste oblongae apice rotundatae margine minute dense puberulae extus plerumque trisulcatae superne in bracteis interioribus sensim dense puberulae; receptacula leviter convexa sparse puberula interne non scleroidea. Flores ca. 25; corollae albae tubulosae ca. 3 mm longae; faucis tubulosis base indistinctis glabris, lobis triangularibus ca. 0.4 mm longis et latis extus dense minute puberulis, pilis brevibus in apicem subclavatis; filamenta in parte superiore ca. 0.15 mm longa; thecae ca. 0.8 mm longae; appendices antherarum late oblongae ca. 0.15 mm longae et latae; grana pollinis ca. 20 mμ in diametro; achaenia 1.5 mm longa sparse minute glandulifera superne pauce sed non breviter setifera; setae pappi ca. 45 plerumque ca. 2.5 mm longae ad apicem vix vel non latiores, cellulis apicalibus obtusis.

TYPE: COLOMBIA. CHOCÓ: Alto de Buey, 1,200–1,800 m, tropical wet forest, weak-stemmed shrub, flowers white, 8 Jan. 1973. *Al Gentry & Enrique Forero 7290* (US, holotype; MO, isotype).

Hebeclinium gentryi is most closely related to *H. reedii* R. M. King & H. Robinson (King & Robinson, 1972) of adjacent Darién Province of Panama. The two species share the lanate stems, the pubescent outer surfaces of the involucral bracts, less hemispherical receptacles than usual in the genus, and

FIGURE 2. *Hebeclinium gentryi* R. M. King & H. Robinson, holotype, United States National Herbarium.

leaves with at least partially doubly serrate margins. The new species does have a different appearance from *H. reedii* by the smaller leaves and the more neatly oblong subimbricate involucral bracts, but the more significant differences are the glabrous to glabrescent upper leaf surfaces, the less pubescent

surface and larger area of pith on the receptacles, the scarcely enlarged tips of the pappus setae, and the glanduliferous achenes. In *H. reedii* the upper surfaces of the leaves are coarsely pilose, the receptacles are shortly but densely puberulous on the ridges, the pith of the receptacles is very reduced, the pappus setae have prominently enlarged tips, and the achenes are glabrous.

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NOTES

A NEW SPECIES OF *BAUHINIA* (*LEGUMINOSAE*) FROM PERU

Continued revisionary studies of the neotropical species of *Bauhinia* have resulted in the discovery of a new species of the genus endemic to Peru.

Bauhinia hirsutissima Wunderlin, sp. nov.

Frutex scandens cirrhosus; rami juvenales fuscoporphyro-hirsuti. Folia anguste ovata ad oblonga, ca. ⅓ vel rare ⅔ longitudine bilobata, 5–14 cm longa, 4–10 cm lata, apice acuminata ad obtusa, basi profunde cordata, margine revoluta, chartacea ad subcoriacea, supra glabra, infra fuscoporphyro-hirsuta, 9- ad 11-nervata; petioli 3–5(–7) cm longi; stipulae reniformes. Inflorescentiae racemosae, terminales vel subterminales et axillares, graciles, laxae, fuscoporphyro-hirsutae; rhachis 12–40 cm longa; gemmae ovoideae, excrescentibus apicalibus gemmarum ovato-lanceolatis, 3–5 mm longis, incurvatis; bracteae et bracteolae anguste lanceolatae, 5–7 mm longae; pedicelli graciles, 5–10 mm longi; hypanthium cyathiforme ca. 1 mm longum; calyx campanulatus vel leviter biblabiatus, 15-nervatus; petala 5, subaequalia, alba vel subrosea, 10–12 mm longa, lamina late elliptica, intra glabra, extra dense adpresso-pilosa, ungue lamina longiore vel subaequalia; stamina fertilia 10, tubo calycis longitudine subaequalia, libra, 5 glabra, 5 versus apicem pilosa, antheris oblongis, ca. 1 mm longis; gynoecium staminibus longitudine plus minusve aequale, stylo brevi, crasso, arcuato, glabro, ovario dense hirsuto, gynophoro minuto, stigmate obliquo. Legumen dehiscens, oblongum ad anguste obovatum, apiculatum, ca. 7.5 cm longum, ca. 2.5 cm latum, brunneum glabratum; semina suborbiculata, 11–12 diam., pagina hebetata puncticulata, obscure striata, brunnea, cicatricibus funiculi ramorum longitudine subaequalibus, ca. 1 mm longa.

Tendriled woody vine; young branches reddish brown hirsute, glabrescent in age, older stems not seen; intrastipular tendrils single or paired, woody, circinate. Leaves narrowly ovate to oblong, bilobate ca. ⅓ or rarely ⅔ their length, 5–14 cm long, 4–10 cm wide, the apex of lobes acuminate to obtuse, the base deeply cordate, the margin revolute, chartaceous to subcoriaceous, glabrous above, reddish brown hirsute below, the lower surface frequently purplish-tinged, 9–11-nerved; petioles 3–5(–7) cm long, reddish brown hirsute; stipules reniform, 5–10 mm long, 2–5 mm wide; intrastipular excrescences other than tendrils minute. Inflorescences racemose, terminal or subterminal and axillary, elongate, slender, lax, reddish brown hirsute throughout; rachis 12–40 cm long, the lower flowers soon deciduous, the inflorescence then frequently with 10–30 flowers on a long-pedunculoid rachis; buds ovoid, 6–8 mm long, the free tips ovate-lanceolate, 3–5 mm long, incurved; bracts narrowly lanceolate, 5–7 mm long; bracteoles similar to the bracts, but smaller, attached near or above the middle of the pedicel; pedicels slender, 5–10 mm long; hypanthium cyathiform, ca. 1 mm long; calyx campanulate or slightly bilabioid at anthesis, 15-nerved, each trio of nerves ending at one of 5 ovate-lanceolate appendages at the rim of the calyx tube, the median nerve extending the length of appendage, the lateral 2 ending at the base of the appendage or inconspicuously extending up to ½ its length; petals 5, subequal, white or faintly tinged with pink, 10–12 mm long, the blade broadly elliptic, 5–7 mm long, 3–4 mm wide, glabrous internally, densely appressed brown-pilose externally, the claw longer than to nearly equal-

ling the length of the blade, brown pilose; fertile stamens 10, ± equalling the calyx tube, free to the base, alternate ones slightly shorter, the longer 5 glabrous, shorter 5 brown pilose towards the tip, the filaments arcuate, the anthers oblong, ca. 1 mm long, white-pilose; gynoecium ± equalling the stamens, the style short, thick, arcuate, glabrous, the ovary densely brown-hirsute, the gynophore not evident, the stigma oblique, slightly differentiated from the style. Fruit a dehiscent legume, oblong to narrowly obovate, apiculate with a persistent style, ca. 7.5 cm long, ca. 2.5 cm wide, dark brown, glabrate, gynophore not seen; seeds suborbicular, ca. 12 mm long, ca. 11 mm wide, the surface dull, puncticulate, obscurely striate, dark brown, funicular-branch scars subequal, ca. 1 mm long. Chromosome number unknown.

TYPE: PERU. LORETO: Fortaleza, near Yurimaguas, ca. 140 m, forest, Dec. 1932, *G. Klug 2800* (US, holotype; F, MO, NY, isotypes).

Specimens examined: PERU. LORETO: Quebrada Shanuce above Yurimaguas, *Croat 18065* (MO, duplicates to be distributed). Lower Río Huallaga, *Killip & Smith 27601* (F, NY, US), *28302* (F, NY, US). Fortaleza, Yurimaguas, *Ll. Williams 4216* (F, US), *4485* (F, US).

Distribution: Known only from near Yurimaguas on the Río Huallaga, Loreto, Peru. It occurs in forests at elevations of about 140 meters. Flowering material has been collected from July through December with nearly mature fruiting material collected in December.

The newly described species is most closely related to the widespread and highly variable *B. glabra* Jacq., but is distinguished by the following combination of characters: young branches, inflorescences, and lower leaf surfaces conspicuously deep reddish-brown hirsute; inflorescences elongate, slender, lax, with flowers distantly arranged; flower buds ovate, with incurved lanceolate apical excrescences; petal blades 5–7(–8) mm long, without purple spots. In contrast, the vestiture of *B. glabra*, when approaching that of *B. hirsutissima*, is pilose and has a coppery sheen. One local race of *B. glabra* whose pubescence is very similar to that of *B. hirsutissima* is restricted to Panama and differs in all other respects. The flowers of *B. glabra* have petal blades 10–20 mm long, one of which is usually conspicuously marked with purple spots, although sometimes obscure in local races. In *B. glabra* the flower buds are lanceolate with setiform or rarely lanceolate apical excrescences and the inflorescences, if elongate, are strict and with the flowers more closely arranged.

Bauhinia reflexa Schery, a Panamanian and Colombian species, has the vestiture of its leaves, young branches, and inflorescence rachis in addition to the purple-tinged undersides of its leaves like *B. hirsutissima*, but differs in all other respects.

Finally, *B. hirsutissima* also superficially resembles *B. killipiana* Standley and to a lesser degree *B. vulpina* Rusby and *B. porphyrotricha* Harms, but differs slightly in nearly all characters. Specimens determined to be *B. hirsutissima* have frequently been identified by other workers as *B. porphyrotricha*. Examination of type material of *B. killipiana*, *B. vulpina*, and *B. porphyrotricha* reveal that these species are best placed in synonymy with *B. glabra* sensu lato.

I gratefully acknowledge John D. Dwyer, St. Louis University and Missouri Botanical Garden for critically reading the manuscript, especially the Latin description, and the curators of the herbaria who loaned specimens for this study.

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ALNUS MARITIMA MUHL. EX NUTT., NOT *ALNUS METOPORINA* FURLOW

The new name, *Alnus metoporina* Furlow, proposed in a recent issue of this journal (Furlow, 1976) to replace the long-recognized *Alnus maritima* Muhl. ex Nutt., is unnecessary according to Article 55 of the International Code of Botanical Nomenclature (Stafleu et al., 1972) which states:

> When a species is transferred to another genus or placed under another generic name for the same genus without change of rank, the specific epithet, if legitimate, must be retained or, if it has not been retained, must be reinstated unless one of the following obstacles exists:
> (1) The resulting binary name is a later homonym (Art. 64) or a tautonym (Art. 23).
> (2) An earlier legitimate specific epithet is available (but see Arts. 13f, 58, 59, 72).

The genus *Betula-Alnus* was validly published by Humphry Marshall in his *Arbustrum Americanum* (1785), and three species, including *B. maritima*, placed in it. Marshall's description of *B. maritima* is sketchy, mentioning only the height of the plant, the "long and narrow" leaves, and the very distinctive August anthesis. Marshall did not cite a type nor did he keep an herbarium, and so we do not know on what material the species was based. However, we have no doubt that the plant was the same species that was later described by Henry Muhlenberg in an unpublished manuscript, and subsequently validly published by Thomas Nuttall (1842) in the first volume of his *Sylva*. *Alnus maritima* was described as a new species in the genus *Alnus*, based not upon Marshall's name [as assumed by some authors, see Little (1953)] but upon Muhlenberg's manuscript name.

We know that Muhlenberg was well acquainted with Marshall's work for in a letter to William Bartram dated 10 December 1792 (Darlington, 1849), he wrote: "Marshall has given me some satisfaction, but his Arbustrum wants some emendations. Any observations that way where you think he is wrong, or where another name might have been given, would be so pleasing to me."

It is likely that Muhlenberg may have recognized that his species was *Betula-Alnus maritima* of Marshall, and that he intended to make the transfer to *Alnus*, and to typify the species on the Bartram collection he had. However, there is nothing in the manuscript preserved at the Philadelphia Academy of Sciences Library to suggest this, and we may only speculate on Muhlenberg's intentions.

Nuttall apparently put even less faith in Marshall's work, for he never mentioned it directly in the first volume of his *Sylva*. Marshall is cited there only once, and then in synonymy under Nuttall's *Carya microcarpa*. Since a Muhlen-

berg synonym is also cited, it is possible that the Marshall reference was copied by Nuttall from Muhlenberg.

Furlow (1976) is correct in his contention that to transfer Marshall's earlier epithet from *Betula-Alnus* to *Alnus* would create a later homonym (prohibited by Articles 55[1] and 64). His creation of a new name for *B. maritima* to avoid the creation of a homonym, however, is not correct. Article 55(2) requires that if an earlier legitimate specific epithet is available for the species, it must be adopted. *Alnus maritima* as proposed by Nuttall (1842) is legitimate, is available, and antedates Furlow's *A. metoporina*. *Alnus maritima* Muhl. ex Nutt. must be retained for this plant.

We propose to lectotypify *Alnus maritima* on the Pickering specimen (PH) on which Nuttall's (1842) description and Plate X (bis) were based, and not on the Bartram specimen (#477 in Herb. Muhlenberg, PH) which was also seen and indirectly mentioned by Nuttall. Furlow has supplied a neotype for Marshall's *Betula-Alnus maritima*.

We would like to thank the staff at the Philadelphia Academy of Sciences for their many courtesies, and Dr. Dan H. Nicolson of the National Museum of Natural History, Smithsonian Institution, for his advice on the provisions of the Code discussed herein.

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NEW TAXA AND COMBINATIONS IN THE GENUS *LASIACIS* (GRAMINEAE)

The following new taxa and new combinations are published in advance of my systematic treatment of the genus *Lasiacis* in order to make them available for use in other publications. A new species, *Lasiacis nigra* Davidse, has also been published (Davidse, 1974). Full explanations for my treatment will be given in the forthcoming publication.

Lasiacis divaricata (L.) Hitchc. var. **austroamericana** Davidse, var. nov.

Ab *L. divaricata* var. *divaricata* spiculis globosis et ramis paniculae ascendentibus differt.

TYPE: BRAZIL. MINAS GERAIS: Near Santa Barbara do Caparaco, streamside, suffrutescent, 3 m high, climbing and rooting at lower joints, "canaviera," 21 Nov. 1929, *Mexia 4007* (NY, holotype; F, GH, UC, US, isotypes).

Lasiacis divaricata (L.) Hitchc. var. **leptostachya** (Hitchc.) Davidse, comb. et stat. nov.

Lasiacis leptostachya Hitchc., Contr. U.S. Natl. Herb. 22: 19. 1920. TYPE: NICARAGUA. Jinotepe, jungle, 500 m, stout central canes, branches more or less whorled and slender, floral branches conspicuously flexuous, panicles all small, 7 Nov. 1911, *Hitchcock 8718* (US, holotype).

Lasiacis grisebachii (Nash) Hitchc. var. **lindelieana** Davidse, var. nov.
Ab *L. grisebachii* var. *grisebachii* laminis latioribus (1.5–2.0 cm) differt.

TYPE: CUBA. HABANA: Lomas de Camoa, in siloa locis umbrasis satis frequens, 27 Nov. 1921, *Ekman 13530* (US-1295003, holotype; F, NY, US-1502317, isotypes).

Lasiacis oaxacensis (Griseb.) Hitchc. var. **maxonii** (Swallen) Davidse, comb. et stat. nov.

Lasiacis maxonii Swallen, Ann. Missouri Bot. Gard. 30: 231. 1943. TYPE: PANAMA. CHIRIQUÍ: Vicinity of El Boquete, in thickets along wet trail, 1,000–1,300 m, 2–8 Mar. 1911, *Maxon 4999* (US, holotype; US, isotype).

Lasiacis rugelii (Griseb.) Hitchc. var. **pohlii** Davidse, var. nov.
Ab *L. rugelii* var. *rugelii* spiculis globosis minoribus, inflorescentiis minoribus, ramis paniculae ascendentibus vel patentibus, pseudopetiolis amplis differt.

TYPE: COSTA RICA. CARTAGO: 1 km NE of Pejibaye, along Río Pejibaye, growing at base of tree, ca. 700 m, 2 Nov. 1968, *Pohl & Davidse 11478* (ISC, holotype; CR, EAP, K, MO, US, isotypes).

Lasiacis ruscifolia (H.B.K.) Hitchc. var. **velutina** (Swallen) Davidse, comb. et stat. nov.

Lasiacis velutina Swallen, Ceiba 4: 288. 1955. TYPE: HONDURAS. MORAZÁN: Vicinity of El Zamorano, road to San Antonio, 17 Oct. 1951, *Swallen 10834* (US, holotype).

Lasiacis sorghoidea (Desv.) Hitchc. & Chase var. **patentiflora** (Hitchc. & Chase) Davidse, comb. et stat. nov.

Lasiacis patentiflora Hitchc. & Chase, Contr. U.S. Natl. Herb. 18: 338. 1917. TYPE: TOBAGO: Center of island, edge of woods on mountainside, 20 Dec. 1912, *Hitchcock 10268* (US-865566, holotype; US-975660, isotype).

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—*Gerrit Davidse, Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.*

SOLANUM ARMENTALIS: A NEW SPECIES FROM COSTA RICA

Solanum armentalis J. L. Gentry & D'Arcy, sp. nov.—FIG. 1.

Frutex 1 m altus inermis omnino confertim stellato-pubescens, trichomatibus fulvis, sessilibus, radio medio quam radiis lateralibus multo longiore; foliis singularibus vel in geminis inaequalibus, pilis subtus creberrimis, supra sparsis praeter secus costam; foliis majoribus ovatis vel ovato-ellipticis, 13–14 cm longis, 6–7 cm latis, apice longo-acuminatis, basim rotundis, petiolo 5–7 mm longo; foliis minoribus ovatis vel late ellipticis; inflorescentia lateralibus foliis opposita, pedunculo supra 5 cm bifurcato; floribus parvis, calyce 2–2.5 mm longo prope basim fisso, lobis ovatis, 1.5–2.2 mm longis, apice acutis, staminibus aequalibus, filamentis glabris, basim connatis, antheris 2.5 mm longis, poris largis terminalibus aperientibus, ovario glabro, stylo glabro; acino ignoto.

Shrub 1 m tall, unarmed, densely stellate-pubescent throughout, the hairs sessile, yellowish brown with the central ray greatly exceeding the lateral rays. *Leaves* solitary or in pairs, unequal in size, similar or different in shape, densely pubescent beneath, sparsely pubescent above except along the midvein; larger leaves ovate to ovate-elliptic, the blade 13–14 cm long, 6–7 cm wide, the apex long acuminate, the base rounded, the petiole 5–7 mm long; smaller leaves ovate to broadly elliptic, the blade 1.8–4 cm long, 1.2–2.8 cm wide, the petiole 2–3 mm long. *Inflorescence* both lateral and opposite the leaves, several flowered; peduncle unbranched for 5 cm, bifurcate; pedicels slender, 10–12 mm long. *Flowers* small; calyx 2–2.5 mm long, parted to near the base, the lobes ovate, 1.5–2 mm long, the apex acute; corolla white, the limb 10–11 mm wide, parted to near the base, the lobes 4–4.5 mm long with sessile stellate pubescence externally; stamens equal, the filaments glabrous, ca. 0.7 mm long, basally connate, the anthers 2.5 mm long, the pores large; ovary glabrous, the style glabrous, exceeding the stamens. *Fruit* unknown.

TYPE: COSTA RICA. PROV. PUNTARENAS: Open forest 1 mi due south of San Vito de Java, ca. 3500 ft., 18 Aug. 1967, *Peter H. Raven 21887* (MO-2304198, holotype; F, isotype).

Additional collection examined: COSTA RICA. PROV. SAN JOSÉ: Vicinity of El General, edge of forest, 700 m, Jan. 1939, *Alexander F. Skutch 3919* (MO).

Solanum armentalis is recognized from other species of the genus in the Central American flora by the softly tomentose leaf undersides, long, slender peduncles and slender pedicels, and small white flowers which have calyces divided nearly to the base. The indumentum is of dense, sessile stellate hairs, with the midpoints many times longer than the several short lateral arms.

This species is a member of subgenus *Brevantherum.* However, it is not easily placed in a section within the subgenus. At first glance the plant is suggestive of *Solanum extensum* Bitt. and *S. cordovense* Sessé & Moç., but the calyx is different in shape and not accrescent to judge from the one immature fruit on the Skutch specimen. Also, the indumentum and inflorescence are different. *Solanum gemellum* Sendt. and *S. megalochiton* Mart. of eastern Brasil have calyces similar in shape, but they are conspicuously accrescent in fruit. While the above similarities are suggested, they do not imply a close relationship to the species described here.

FIGURE 1. *Solanum armentalis* J. L. Gentry & D'Arcy.—A. Flowering branch (×½).—B. Stem showing stellate hairs (×3).—C. Flower (×2½). [After *Raven 21887* (MO).]

It has been collected twice in Costa Rica, at 700 and 1,165 m elevation on the Pacific side of the isthmus. Perhaps further collections will provide an insight into its ecological requirements. The locality of San Vito suggests that this species may be found in the nearby Chiriquí Mountains of Panama.

Because no single character delimits this well-marked species, the specific epithet does not relate to the collector, collection locality, or morphological features.

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HERBERTIA (IRIDACEAE) REINSTATED AS A VALID GENERIC NAME

The genus *Herbertia* was described in 1827 by Robert Sweet for a New World genus of Iridaceae. As currently circumscribed (Goldblatt, 1975), the genus is a small one of approximately six species centered in temperate South America from Uruguay to Chile with a subspecies of a South American taxon occurring in the southern United States.

The existence of the similar name *Herbertus* Gray (also used in the form *Herberta*) published in 1821, prompted several authors including myself to regard *Herbertia* as a later homonym and therefore to reject it. Following Kuntze (1898) who first suggested that *Herbertia* be considered a homonym, both Foster (1945) and Ravenna (1968) among others, accepted *Alophia* Herb. (dating from 1840) as the valid name for the genus. Subsequently I discovered (Goldblatt, 1975) that the type species of *Alophia* had been misinterpreted and was in fact a species of what was then known as *Eustylis*. I therefore proposed another available synonym of *Herbertia*, namely *Trifurcia* Herb., for the genus and provided new combinations in *Trifurcia* for both the United States subspecies and for the South American representatives of *Herbertia*.

Recently it has been suggested both in print (Florschutz & Grolle 1975) and to me personally that *Herbertia* should not have been rejected and that I should carefully consider Article 75 of the *Botanical Code of Nomenclature*. This article deals with names of similar but not identical spelling, and recommends rejection only in cases of likely confusion. The article recommends the rejection of examples such as *Columella* and *Columellia* and *Eschweilera* and *Eschweileria* as being too similar and thus likely to cause confusion. Other examples are *Peltophorum* and *Peltophorus*, *Iria* and *Iris*, neither of which are to be considered homonyms and therefore both forms of these words are available for usage for different genera.

Herbertia seems to fall into the latter category, being sufficiently different in orthography to avoid any possibility of confusion. Florshutz & Grolle (1975) support this view, as do several colleagues with whom I have discussed the

question. Therefore, I propose reinstatement of *Herbertia* and the synonymizing of *Trifurcia*. This treatment involves some new combinations as follows:

1. **Herbertia lahue** (Molina) Goldbl., comb. nov. Basionym: *Ferraria lahue*, Molina, Sagg. Stor. Nat. Chile, ed. 2: 110. 1810.

The subspecies of this taxon are to be cited as follows:

1a. **H. lahue** subsp. **amoena** (Griseb.) Goldbl., comb. nov. Basionym: *Herbertia amoena* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 325. 1879.
1b. **H. lahue** subsp. **caerulea** (Herb.) Goldbl., comb. nov. Basionym: *Trifurcia caerulea* Herb., Bot. Mag. 1840: *tab. 3779*. 1840.
2. **Herbertia tigridioides** (Hick.) Goldbl., comb. nov. Basionym: *Alophia tigridioides* Hick., Darwiniana 1: 116. 1924.

The four remaining species were either originally placed in *Herbertia*, or have in the past been transferred to the genus. These are: *H. pulchella* Sweet, *H. amatorum* C. H. Wright, *H. hauthallii* (O. Kuntze) K. Schum, *H. brasiliensis* Baker.

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SYSTEMATICS OF *OENOTHERA* SECT. *KNEIFFIA* (ONAGRACEAE)[1]

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ABSTRACT

Based on cytology, morphology and field studies, a reevaluation of *Oenothera* sect. *Kneiffia*, the eastern North American day-flowering oenotheras or sundrops, is presented, with five species recognized. Subsect. *Peniophyllum* contains a single annual species, *O. linifolia*, of the southeastern United States, which is a self-compatible diploid ($n = 7$). Subsect. *Eukneiffia* contains one annual self-compatible diploid ($n = 7$), *O. spachiana*, largely of the southern Mississippi Valley, and three perennials, *O. perennis*, *O. fruticosa*, and *O. pilosella*. *Oenothera perennis* is a self-compatible diploid ($n = 7$), complex heterozygote, forming a ring of 14 chromosomes at meiotic metaphase I and having about 50% pollen sterility. It is distributed from Newfoundland to Manitoba and south to North Carolina and Missouri. The two other perennials, each with two subspecies, are self-incompatible polyploids that seem to lack chromosomal translocations but form numerous rings of chromosomes at meiotic metaphase I owing to their autopolyploidy. *Oenothera pilosella* subsp. *pilosella*, a taxon largely of the midwestern United States, is known only as an octoploid ($n = 28$). *Oenothera pilosella* subsp. *sessilis*, also octoploid, is treated as a second subspecies. It is very rare at present and is found in remnant prairies of the lower Mississippi River Valley. It differs from subsp. *pilosella*

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in being nonrhizomatous; it has narrower, ascending leaves, more ellipsoid, nearly sessile capsules, and strigose pubescence throughout. The widespread polymorphic *O. fruticosa* consists of a more southern and lower elevation subspecies, subsp. *fruticosa*, which is tetraploid ($n = 14$) and hexaploid ($n = 21$), and a more northern and higher elevation subspecies, subsp. *glauca* (*O. tetragona* Roth), which as far as known is entirely tetraploid.

The Onagraceous genus *Oenothera* has been the subject of classical studies of reciprocal translocations and their effects on the evolution of a group of plants. Much of the early cytogenetic and cytotaxonomic work was done on the North American species of sect. *Oenothera* (Cleland, 1972). Other portions of the genus have received less attention, but studies of *Raimannia* (Hecht, 1950), of several subgenera by Hagen (1950) and Gregory & Klein (1960), and of the South American species of sect. *Oenothera* by Dietrich (1977) are among the most important works. Subgenera are treated in this paper as sections consistent with the classification employed elsewhere in the family (Lewis & Lewis, 1955; Raven, 1964; Raven & Gregory, 1972b).

Oenothera sect. *Kneiffia* has received little biosystematic attention. Taxonomic treatments of *Kneiffia* based largely on morphological characters have resulted in a confusing array of specific, subspecific, varietal, and form names. Even the most recent, rather thorough revision based upon morphological features by Munz (1965) reflects the difficulties in circumscribing species and particularly in delimiting infraspecific taxa. A recent biometrical and biochemical study (DeTurck, 1969) has also failed to clarify the taxonomic problems in this section. Records of chromosome numbers and meiotic pairing in species of sect. *Kneiffia* are few and scattered in the literature, and many of these, particularly the older records, are from plants grown in botanical gardens for which the original source of material is not known, and for which no voucher specimens were made. There are no previous reports of complex heterozygosity in sect. *Kneiffia*, although polyploidy has been reported a number of times, especially by Gregory & Klein (1960) and by Laws (1963).

Plants in this section are characterized by bright yellow flowers that open after sunrise, relatively short floral tubes, and 4-angled to 4-winged fruits borne on a short stipe. They are distributed from Newfoundland to northern Florida and westward to southeastern Manitoba and eastern Texas. Natural populations usually have easily discernable limits, particularly in the perennial species, and are commonly composed of a few to rarely more than several dozen plants. The two annual species tend to be found in scattered populations with less distinct boundaries.

Materials and Methods

This study was begun in 1973, initially in an effort to evaluate the cytology of the section as a basis for understanding the morphological discontinuities, particularly among the perennial species. Extensive field studies were made from 1973 to 1976 throughout much of the distribution of the section. Vouchers are deposited at MO.

Flower buds were fixed in the field in 1:3 glacial acetic acid : ethanol and

later transferred to 95% ethanol and refrigerated. The buds were hydrolyzed in 1:1 concentrated hydrochloric acid : 95% ethanol at room temperature until they were translucent (10–20 minutes depending on bud size) to remove starch grains from the pollen mother cells (Lewis & Lewis, 1955). After hydrolysis, the anthers were removed, stained with aceto-carmine and macerated with iron needles. A drop of Hoyer's medium (Beeks, 1955) was added to make the slide permanent. The preparation was squashed and later the coverslip was ringed with Diaphane. Observations of meiotic divisions of microsporocytes were made during diakinesis or metaphase I using a positive phase-contrast microscope.

Pollination systems and floral biology were studied in several natural populations, and seeds or plants were collected and grown in the greenhouse or experimental garden for compatibility studies and further observation of characters. Field collections have been supplemented by examination of over 11,000 herbarium specimens, including large enough samples of all taxa to be of great value in comparative morphology. Where available, herbarium voucher specimens and permanent slides of cytological material from previously reported chromosome studies of sect. *Kneiffia* were borrowed for further study.

Based on a reevaluation of morphological characters and the results of cytological and breeding studies, a revised classification of the taxa is presented here.

Historical and Taxonomic Considerations

Due to their widespread distribution and abundance in eastern North America, the species of sect. *Kneiffia* have been the subject of study for more than 200 years. Linnaeus described the first species, *Oenothera perennis*, in 1753. The classification of this group subsequently has undergone many reorganizations owing to the difficulties in assigning populations to clear-cut morphological species. The greatest taxonomic problems are in the two perennial, polyploid species treated by Munz (1965) and in most recent floras (e.g., Gleason, 1963; Fernald, 1950; Radford et al., 1968) as *O. fruticosa* L. and *O. tetragona* Roth, including *O. glauca* Michx. [= *O. fruticosa* L. subsp. *fruticosa* and *O. fruticosa* L. subsp. *glauca* (Michx.) Straley, respectively, in this treatment].

In early studies of the section (e.g., Michaux, 1803; Pursh, 1814) *O. glauca*, with broader leaves, glandular hairs, and oblong capsules, was considered distinct from *O. fruticosa*, with narrower leaves, nonglandular hairs, and distinctly clavate capsules. At this time, there was a paucity of herbarium material available for study and few, if any, intermediate populations had been sampled. Later, as more material became available, Spach (1835), Torrey & Gray (1838–1840), Small (1896), and Léveillé (1902), in accord with the trends of the times, assigned taxonomic status to more of the intermediate populations, giving them specific, varietal, or form rank. Watson (1873), however, took a more conservative view, recognizing only *O. fruticosa* and *O. glauca*. Pennell (1919) in the first thorough study of the group, recognized nine species with three varieties within this species complex. He was clearly not completely satisfied with his taxonomic treatment, however, as shown by his statement, "I present the results of this study with hesitation. Species lines have not always been found clear,

and in any genus so near to *Oenothera* one may expect the same tendency to split into incipient species" (Pennell, 1919: 363).

Munz (1937) simplified the classification of this group by recognizing only the two species in the complex, but he retained 12 infraspecific entities; in 1965, Munz still recognized only two species, with 10 infraspecific entities, and stated that the two were in need of cytological and experimental work.

In regional floras where Munz's treatments are followed closely, comments are often made concerning the variability of the two species (e.g., Fernald, 1950; Gleason, 1963). Radford et al. (1968: 752) say of *O. tetragona*, "This species complex and number 9 [*O. fruticosa*] are poorly understood, both are in need of biosystematic study."

W. J. Hooker (1837, sub *pl. 3545*) was far ahead of his time when he astutely observed that "*O. fruticosa* is a species, widely extended throughout North America from Canada to Carolina; but so variable in its foliage and hairiness, as to suggest the idea of there being the several species above enumerated." In this species he included 10 previously recognized taxa, even the broad-leaved *O. glauca*. At this early date Hooker recognized the variability within this species complex and its essential cohesiveness.

Thus two philosophies have emerged in regard to the systematics of this complex. The one, splitting and assigning formal taxonomic status to many populations, contrasts with the other, lumping populations into taxa with broad species lines. Difficulties in splitting the section into a large number of taxa are caused by the infraspecific variability. Individual plants within one population can be assigned to different taxa, and there are countless morphological intermediates forming a continuum from one taxon to another, making distinct narrow specific lines impractical. Consequently, the treatment here of *O. fruticosa* with two relatively distinct subspecies, both morphologically and geographically, seems the only practical and taxonomically sound means of reflecting the variability found in this species in nature.

Other entities in sect. *Kneiffia* have presented fewer taxonomic difficulties. *Oenothera pilosella* Raf. has been considered a variety of *O. fruticosa* in studies of *Oenothera* by Torrey & Gray (1840), Small (1896), and Léveillé (1902), but since Pennell's monograph of *Kneiffia*, it consistently has been recognized as a distinct species. *Oenothera sessilis* (Pennell) Munz, likewise, was first recognized as a species by Pennell (1919), but in light of its close similarities to *O. pilosella*, both in overlapping morphological characteristics and like chromosome number ($n = 28$), it is here assigned to subspecific rank within that species. The remaining three taxa, *O. perennis* L., *O. spachiana* Torr. & A. Gray, and *O. linifolia* Nutt. are morphologically distinct and have caused few taxonomic problems in the past, other than a few inconsequential varieties having been described within these species from time to time.

Discussion of Characters

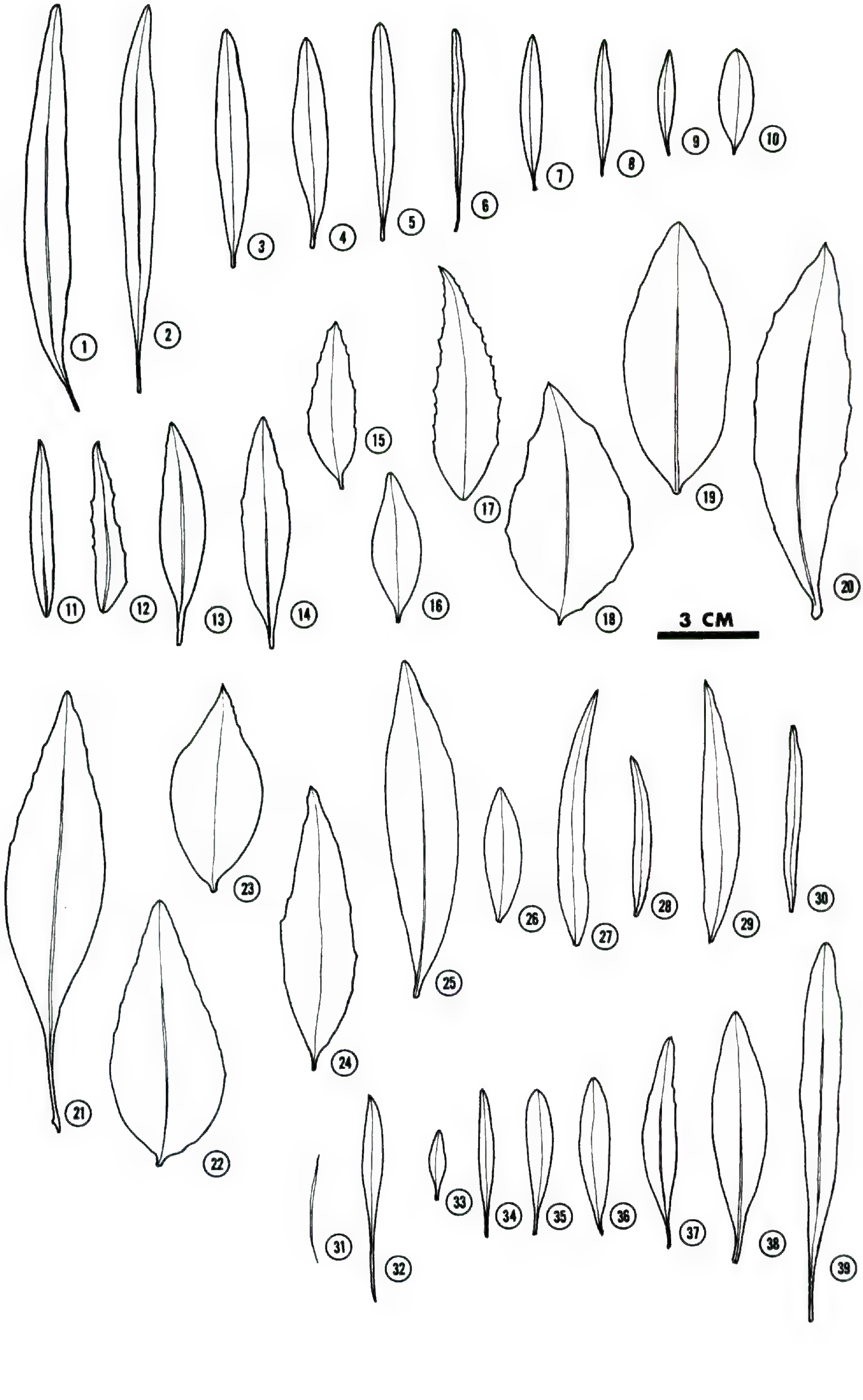
Among the characters used in determining relationships among the species of *Oenothera* sect. *Kneiffia* and in evaluating the phylogeny of the section are the following:

Habit: Two species, *O. linifolia* and *O. spachiana*, are herbaceous annuals; whereas three, *O. fruticosa*, *O. pilosella*, and *O. perennis*, are perennial. A basal rosette of seedling leaves is produced in the annuals soon after germination, whereas an overwintering basal rosette is produced during late summer in the perennials. The rosette in the perennial species may be directly attached to the rootstock of the present year's growth, forming a clump, or at the end of rhizomes several centimeters away from the current year's rootstock, then forming a colony often covering several square meters. The rosettes remain evergreen through the winter and usually wither by early anthesis, although they may remain green during most of the flowering time. The primary stem begins to elongate in early spring as the photoperiod lengthens, only following a period of cold weather. In the perennials the underground base of the stem often becomes swollen and woody, especially in drier habitats. The formation of rhizomes is characteristic of *O. pilosella* subsp. *pilosella*, but rare in *O. fruticosa* subsp. *fruticosa*. A sparsely branched taproot is characteristic of the annuals. Fibrous roots (rarely fleshy in subxeric conditions) are characteristic of the perennial species. Stems are usually erect and are simple to much branched from near the base or above. When the stems become decumbent, they often root at the nodes.

Leaves (Figs. 1–39): The leaves are variable in size, shape, pubescence, and texture. They range from linear or nearly filiform to ovate, with margins subentire to coarsely dentate, and often undulate. The basal leaves are always petiolate with attenuate bases, but the alternate cauline leaves usually become abruptly sessile or short petiolate. The leaves vary from thin and ± translucent to quite thick and leathery, and are occasionally glaucous, especially beneath. The leaves are often dotted, streaked, blotched, or wholly red or purple. They are usually held at right angles to the stem or may be ascending.

Pubescence: Most plants are pubescent throughout. *Oenothera fruticosa* subsp. *glauca* is the only taxon which is often nearly to quite glabrous throughout. In the other taxa stiff erect hairs are frequent near the base of the stem. Higher on the stems the pubescence also may be erect, as in *O. pilosella* subsp. *pilosella*, but it usually is incurved or appressed. The upper parts of the plants, especially the inflorescences, are usually more densely pubescent, with appressed or glandular hairs or a mixture of both. In *O. linifolia*, the pubescence of the inflorescence is puberulent or glandular-puberulent. The basal leaves are usually glabrous except for their ciliate margins. The cauline leaves have less densely ciliate margins. Their surfaces are glabrous to densely strigose or occasionally with erect hairs, usually more pubescent above than below, and usually more densely so along the midribs. Hair color varies from whitish to grey or sometimes, especially in *O. pilosella*, tawny or yellowish. The pubescence varies under different growing conditions. During wet weather or in the relatively humid conditions of the greenhouse, glandular hairs become more frequent on the upper parts of the plant than on the same plant growing under drier conditions. In plants with mixed glandular and nonglandular hairs, the nonglandular ones become more frequent in more xeric conditions.

Inflorescence: Distinct unbranched racemes or corymbs with few to many flowers occur in all but one species. The inflorescences may be either pedunculate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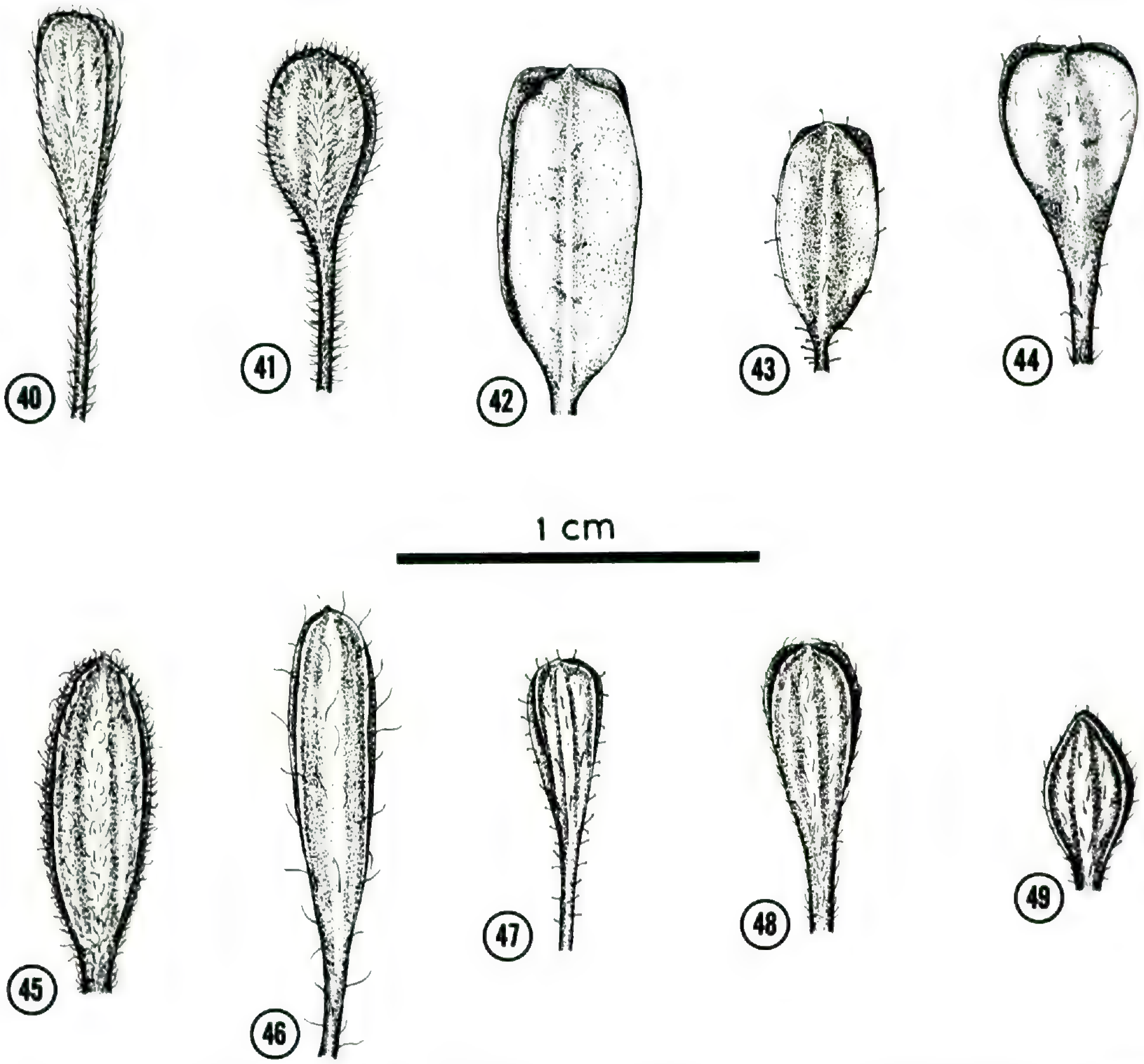
late and sharply distinct or not. The flowers are subtended by small bracts. The tip of the inflorescence in *O. perennis* and occasionally in *O. fruticosa* subsp. *fruticosa* nods and gradually becomes erect as the flowers open. In one annual species, *O. spachiana*, the flowers are borne singly in the axils of normal or slightly reduced cauline leaves on the upper two-thirds or half of the stems; here there appears to be a premium on flowering rapidly following germination.

Flowers and Pollination Systems: The flowers of all species of sect. *Kneiffia* are pale to bright yellow, showy, and very faintly fragrant. Flowering begins in April in the southern portions of the distribution of the section and in June or July in the higher Appalachians and the northern United States and Canada, usually lasting a few weeks to two months, with occasional flowers until frost. The two annual species and one of the perennial species, *O. perennis*, are autogamous, with the style about the same length as the filaments and pollen being shed directly on the enclosed stigmatic lobes often before the flowers open. The three remaining perennial species are allogamous, with the style longer than the filaments and the stigma held above the anthers. The sepals begin to reflex after dark the night before the flower opens and in the outcrossing perennials the stigmatic lobes often extend beyond the still tightly enfolded petals. The petals are probably too tightly folded together to allow any nocturnal pollinators to enter the flowers, even though the pollen usually dehisces during the night, and, at any rate, before the flower opens after sunrise the following morning. The flowers usually remain partially closed on cloudy days and close partially near sunset the first day. They may either wither that first night or reopen for at least six consecutive days before fading. The reflexed calyx often becomes flushed with anthocyanin and pinkish or purplish, as do the petals following pollination. The distal portion of the petals varies from cordate or emarginate to truncate and often undulate, either flat or ± incurved. Cleistogamous flowers are frequently produced in *O. spachiana* and occasionally in *O. linifolia* and *O.*

←

FIGURES 1–39. Outlines of leaves in *Oenothera* sect. *Kneiffia*. Cauline leaves from about a third of the distance up the stem.—1–10. *O. fruticosa* subsp. *fruticosa*.—1. New Hanover Co., NC, *Bell 13047* (VDB).—2. Monroe Co., WV, *Straley 713*.—3. Nottoway Co., VA, *Straley 1072*.—4. Sussex Co., VA, *Straley 705*.—5. Faulkner Co., AR, *Straley 866*.—6. Tuttnall Co., GA, *Straley 919*.—7. Rowan Co., NC, *Straley 725*.—8. McNairy Co., TN, *Straley 960*.—9. Amelia Co., VA, *Straley 1079*.—10. Coffee Co., TN, *Straley 957*.—11–20. *O. fruticosa* subsp. *glauca*.—11. Stark Co., IN, *Deam 94016* (GH).—12. Dade Co., GA, *McVaugh 9041* (MO).—13. Amelia Co., VA, *Straley 1078*.—14. Passaic Co., NJ, *Straley 760*.—15. Passaic Co., NJ, *Straley 1114*.—16. Townes Co., GA, *Duncan 1453*.—17. Stokes Co., NC, *Radford 37678* (GH).—18. Hamilton Co., TN, *Anderson & Jennison 1343* (IA).—19. Mountains of Ky., *Short s.n.* (PH).—20. *Patrick* Co., VA, *Kral 9262* (VDB).—21–28. *O. pilosella* subsp. *pilosella*.—21. Monroe Co., MO, *Hudson 518* (MO).—22. Knox Co., ME, *Straley 787*.—23. Pope Co., AR, *Tucker 15500*.—24. Cleveland Co., AR, *Straley 1069*.—25. Gallia Co., OH, *Straley 925*.—26. Cook Co., IL, *Bebb 2888* (WIS).—27. Union Parish, LA, *Straley 1060*.—28. Drew Co., AR, *Straley 1052*.—29–30. *O. pilosella* subsp. *sessilis*.—29. Arkansas Co., AR, *Straley 1071*.—30. Prairie Co., AR, *Straley 1049*.—31. *O. linifolia*, Lonoke Co., AR, *Straley 1045*.—32. *O. spachiana*, Union Parish, LA, *Straley 751*.—33–39. *O. perennis*.—33. Kings Co., Prince Edward Island, *Straley 1105*.—34. Halifax Co., Nova Scotia, *Straley 1101*.—35. Waldo Co., ME, *Straley 793*.—36. Lamoille Co., VT, *Seymour 29802* (VT).—37. Middlesex Co., MA, *Bean s.n.* (CAN).—38. Essex Co, MA, *Swain s.n* (YALE).—39. Carroll Co., NH, *Straley 827*.



FIGURES 40–49. Capsules of *Oenothera* sect. *Kneiffia*.—40–41. *O. fruticosa* subsp. *fruticosa*.—40. Bland Co., VA, *Straley 754*.—41. Orange Co., NC, *Wiegand s.n.* (F).—42–43. *O. fruticosa* subsp. *glauca*.—42. Wayne Co., WV, *Gilbert & Plymale 715* (US).—43. Kalamazoo Co., MI, *Tuthill s.n.* (GH).—44. *O. fruticosa* near subsp. *fruticosa*, Coffee Co., TN, *Svenson 9168* (POM).—45. *O. pilosella* subsp. *sessilis*, Prairie Co., AR, *Straley 1049*.—46. *O. pilosella* subsp. *pilosella*, Jackson Co., OH, *Straley 750*.—47. *O. perennis*, Colchester Co., Nova Scotia, *Straley 804*.—48. *O. spachiana*, Union Parish, LA, *Straley 751*.—49. *O. linifolia*, Conway Co., AR, *Straley 850*.

perennis. Open flowers of these species are small and rarely visited by insects, although flower flies (Syrphidae) have been observed visiting the flowers of the last two species occasionally. In the larger-flowered perennial species the most frequent insect visitors observed have been bees of the family Halictidae and the genus *Bombus*, butterflies of the families Pieridae and Papilionidae, and skippers (Hesperiidae).

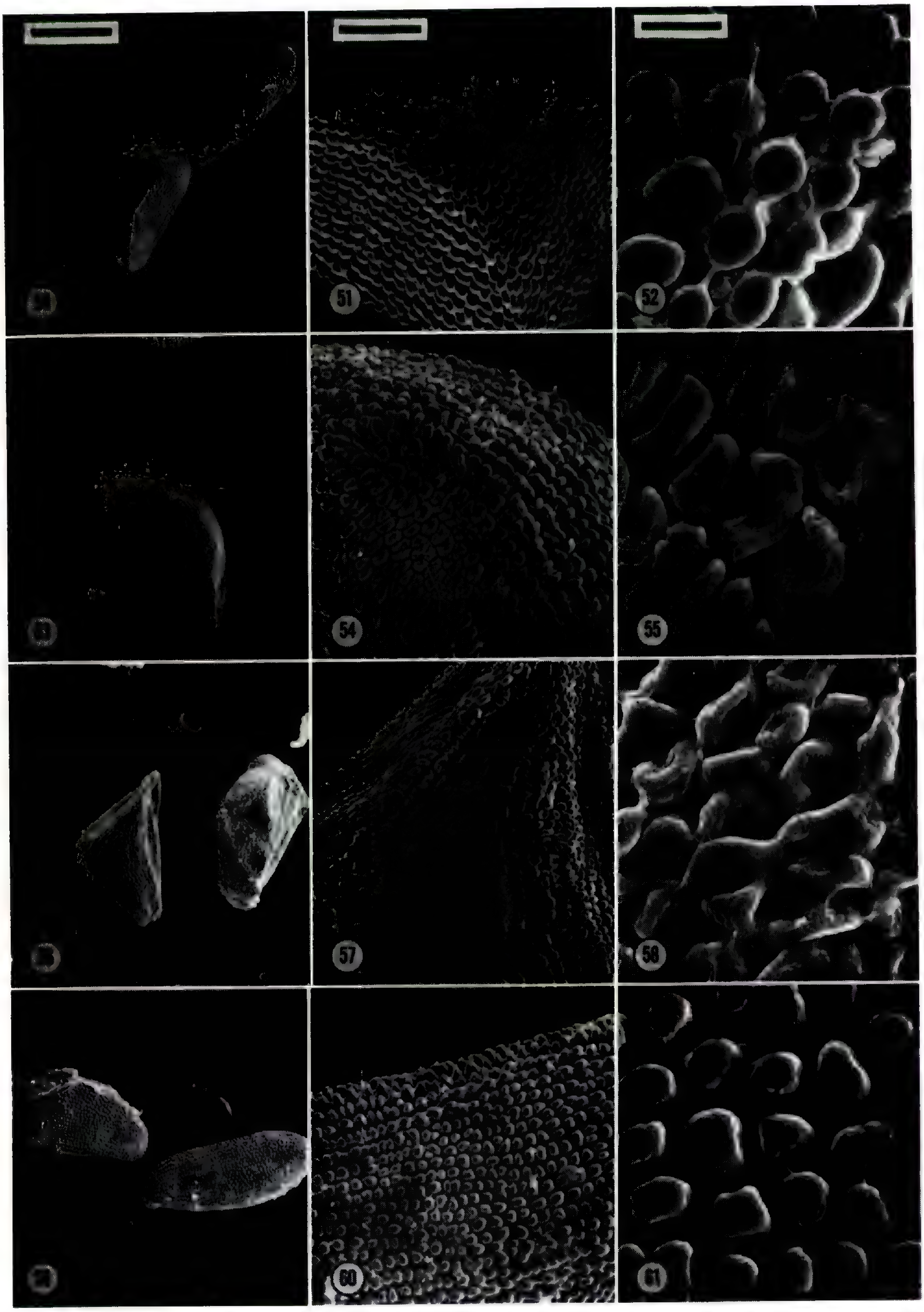
Compatibility: The two annual species, *O. linifolia* and *O. spachiana*, as well as one perennial species, *O. perennis*, were found to be self-compatible. The two remaining species, both perennial, were consistently self-incompatible. Crosses were made using one to several populations of all the perennial taxa except *O. pilosella* subsp. *sessilis*. All crosses among the perennial polyploids

produced mature capsules with full seed set. Crosses between populations of one taxon or different taxa at any one ploidy level produced full seed set, as well as crosses between tetraploids ($n = 14$) and hexaploids ($n = 21$) within *O. fruticosa* and between hexaploid *O. fruticosa* subsp. *fruticosa* and octoploid ($n = 28$) *O. pilosella* subsp. *pilosella*. Crosses utilizing diploid ($n = 7$) *O. perennis* as the female parent with tetraploid *O. fruticosa* as the male parent apparently produced good seed also, but no seed was produced following the reciprocal pollination. De Andrade (1972) reported the spontaneous occurrence of a hybrid between *O. fruticosa* subsp. *glauca* and *O. perennis*, growing near the parents, in cultivation in Torino, Italy.

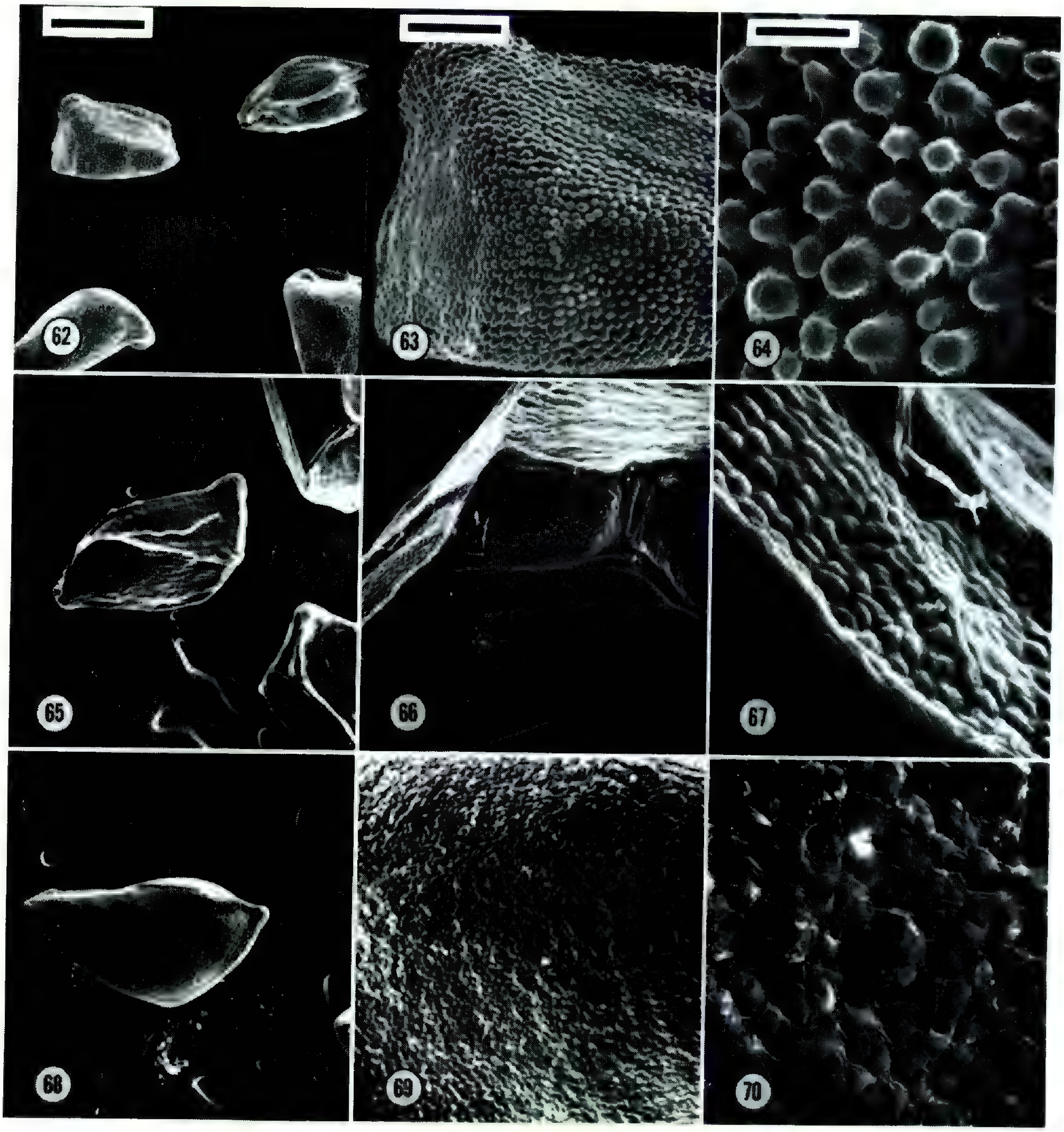
Capsules (Figs. 40–49): These are variable in size, shape, length of stipe, and pubescence, but all are 4-angled to 4-winged, the wings sometimes being quite broad. The shape ranges from ellipsoid-rhomboid in *O. linifolia* to elliptic, linear, or oblong to clavate. The shape and length of the stipe often vary from plant to plant within a given population, from population to population, and from species to species. The capsules dehisce initially only at the distal end, and the seeds are gradually dispersed from the wind- or rain-shaken capsules. Some seeds remain in the capsules and fall to the ground when the plant dies and begins to disintegrate. Dry stems with capsules still attached often remain standing for a year or more, and although the capsules have normally dehisced nearly to the base and partially disintegrated, a few seeds usually remain within. The entire capsule often falls from plants of *O. linifolia* either before or after dehiscence, and it may serve as the unit of dispersal.

Seeds (Figs. 50–70): The seeds are basically ovoid but usually appear very angular due to compression of many other seeds in the capsules. They vary little in size or shape. Under the light microscope they appear smooth to subpapillose, with the papillae in longitudinal rows. Under the scanning electron microscope, the papillae are very pronounced in the perennial species. The surface in *O. linifolia* is obscurely verrucose, and in *O. spachiana* it is verrucose. The seeds of *O. linifolia* are light brown, those of *O. spachiana* pale straw color, and those of the perennial species darker rusty brown. The seeds of *O. spachiana* are somewhat viscid and often adhere to the capsule and other parts of the plant, this doubtless aiding in dispersal.

Chromosome Numbers and Meiotic Configurations (Figs. 71–76): Records of chromosome numbers and meiotic pairing in *Oenothera* sect. *Kneiffia* are few and scattered, and many of these, particularly the older records, are from plants grown in botanical gardens for which the original source of material is not known, and for which no voucher specimens are available. The determinations of the vouchers are often incorrect or questionable, and this poses special problems when vouchers were not made or cannot be located. There are no previous records of complex heterozygosity in sect. *Kneiffia*, although polyploidy has been reported a number of times, notably by Gregory & Klein (1960) and by Laws (1963). The two annual species are diploid, $n = 7$, forming seven pairs at meiotic metaphase I. The small-flowered perennial species, *O. perennis*, is diploid, forming rings of 14 chromosomes at meiotic metaphase I (Fig. 75), and consequently is a complex heterozygote. Since approximately half of its pollen



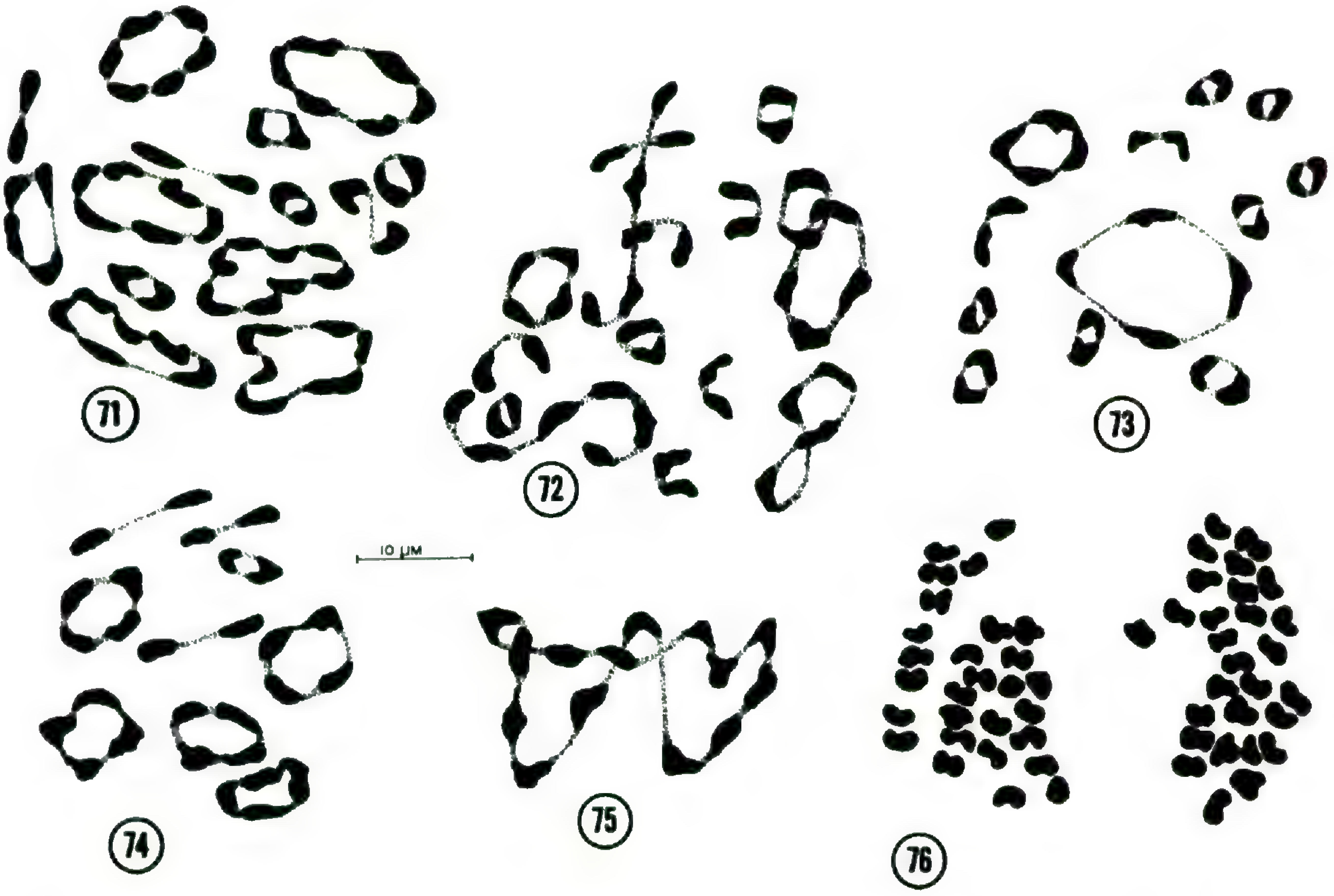
FIGURES 50–61. Scanning electron micrographs of seeds of *Oenothera* sect. *Kneiffia*. The bars at the three levels of magnification represent, respectively, 0.5 mm, 125 μm, and 25 μm.—50–52. *O. fruticosa* subsp. *fruticosa*, Union Co., NC, *Straley 745*.—53–55. *O. fruticosa* subsp. *glauca*, Bedford Co., VA, *Straley 875*.—56–58. *O. pilosella* subsp. *pilosella*, Jackson Co., IL, *SIU-016587*.—59–61. *O. pilosella* subsp. *sessilis*, Arkansas Co., AR, *Straley 1071*.



FIGURES 62–70. Scanning electron micrographs of seeds of *Oenothera* sect. *Kneiffia*. The bars at the three levels of magnification represent, respectively, 0.5 mm, 125 μm, and 25 μm. —62–64. *O. perennis*, Westmorland Co., New Brunswick, *Straley 823*.—65–67. *O. spachiana*, Union Parish, LA, *Straley 751*.—68–70. *O. linifolia*, Conway Co., AR, *Straley 974*.

(32–54%) consists of unfilled grains, it may be assumed that one complex of chromosomes is transmitted through the egg, the other through the sperm. The remaining perennials, here regarded as a complex of two species, are polyploids in which $n = 14$, 21, or 28; no diploids have been found in this group.

Multiple associations of chromosomes in the polyploid species, *O. fruticosa* and *O. pilosella* (Figs. 71–74), could be interpreted as the results of a number of reciprocal translocations; Laws (1963), however, has pointed out the variability in chromosome association from cell to cell and from plant to plant within a population. No associations have been observed of more than four chromosomes in tetraploids, six in hexaploids, and eight in octoploids. This indicates



FIGURES 71–76. Camera lucida drawings of representative chromosomes of *Oenothera* sect. *Kneiffia* during meiosis.—71. *O. pilosella* subsp. *pilosella*, Arkansas, Ashley Co., *Straley 1057*, diakinesis, octoploid with 1 ring of 8, 5 rings of 6, 1 ring of 4, and 7 pairs.—72. *O. fruticosa* subsp. *fruticosa*, Virginia, Virginia Beach, *Straley 701*, diakinesis, hexaploid with 1 chain of 6, 3 rings of 4, 1 chain of 4, and 10 pairs.—73. *O. fruticosa* subsp. *fruticosa*, Alabama, Chambers Co., *Straley 893*, diakinesis, tetraploid with 2 rings of 4 and 10 pairs.—74. *O. fruticosa* subsp. *glauca*, West Virginia, Greenbrier Co., *Straley 758*, diakinesis, tetraploid with 5 rings of 4 and 4 pairs.—75. *O. perennis*, Maine, Knox Co., *Straley 824*, diakinesis, diploid with a ring of 14.—76. *O. pilosella* subsp. *sessilis*, Arkansas Co., Arkansas, *Straley 1071*, anaphase I, octoploid, with 28 chromosomes at each pole of the cell.

these associations are the result of the association of homologous chromosomes, and there has been no positive evidence of the presence of reciprocal translocations. Such translocations, however, were clearly involved in the origin of the complex heterozygote *O. perennis*.

GEOGRAPHY AND ECOLOGY

All taxa are distributed widely in eastern North America, with the exceptions of *O. spachiana* with a relatively narrow range in the lower Midwest and *O. pilosella* subsp. *sessilis* with, at least at present, a very restricted range from southern Arkansas to the Gulf Coast of eastern Texas. All taxa are characteristically plants of somewhat stabilized, previously disturbed habitats, and *O. linifolia* becomes somewhat weedy. The two annual species are characteristic of open fields, prairies, open roadsides, rock outcrops, and sandy places. The perennial species occupy diverse habitats from swampy areas, both fresh and brackish, to the edges of woods, grassy meadows, prairies, and occasionally the edges of bogs and sand dunes. As far as presently known, *O. pilosella* subsp.

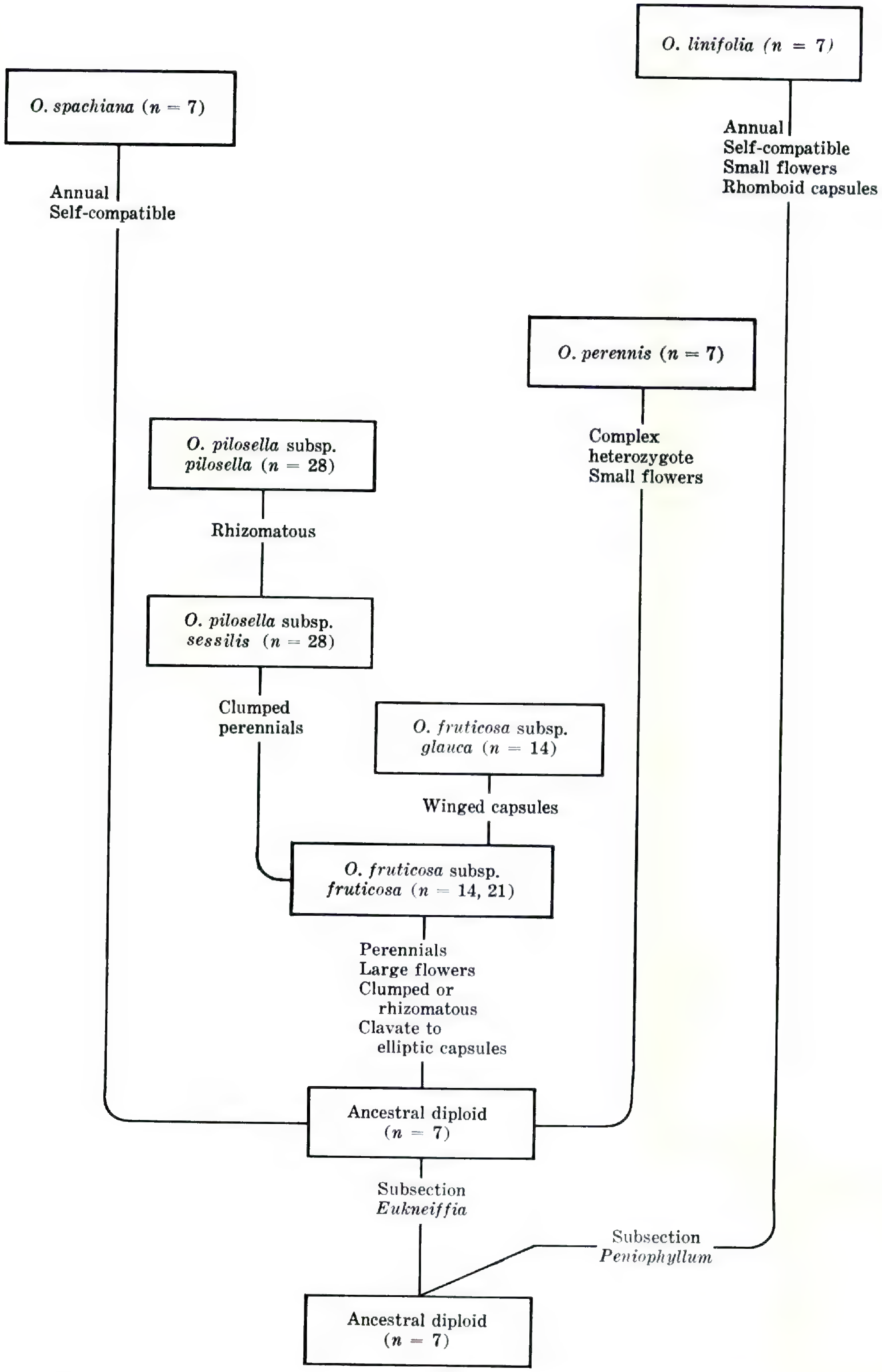


FIGURE 77. Phylogeny of *Oenothera* sect. *Kneiffia.* Gametic chromosome numbers indicated in parentheses.

sessilis is restricted to relatively dry remnant prairies along roads and railroad tracks along the edges of rice fields; it presumably was much more abundant before the advent of widespread agriculture throughout its range.

Phylogenetic Relationships

The phylogenetic relationships within *Oenothera* sect. *Kneiffia* as I conceive them are shown graphically in Fig. 77. Two subsections are clearly recognizable. Subsect. *Peniophyllum* contains a single, clearly specialized species, *Oenothera linifolia*, an annual, self-compatible diploid with small flowers, narrow leaves, and small rhomboid capsules that often serve as the units of dispersal. The remainder of the species with larger flowers, broader leaves, and larger, elongated, stipitate capsules are assigned to subsect. *Eukneiffia*. They are morphologically similar and are thought to have arisen from a common ancestor. The annual, autogamous, diploid *O. spachiana* is considered the most advanced species of this subsection. The remaining species are all clumped or rhizomatous perennials; a clumped habit is considered more primitive than a rhizomatous one. One clumped perennial, *O. perennis*, is, however, in other respects most advanced in its small flowers, autogamy, and complex heterozygosity. Morphological evidence suggests that *O. perennis* may have arisen relatively recently from a common ancestor with *O. fruticosa*.

The remaining perennials apparently exist today only as polyploid populations. Diploids are either rare or extinct. Only tetraploid populations have been found in *O. fruticosa* subsp. *glauca*, with both tetraploids and hexaploids in *O. fruticosa* subsp. *fruticosa*. Hexaploids have probably arisen several times independently as in *Gaura coccinea* Pursh (Raven & Gregory, 1972a, 1972b). The hexaploid populations studied cannot be distinguished morphologically from tetraploids. They seem to be well established and do not have abnormal pollen as in artificially produced polyploids (Hecht, 1942; Laws, 1965).

Oenothera pilosella apparently exists only as octoploid populations, with the rhizomatous *O. pilosella* subsp. *pilosella* being the most specialized of the large-flowered perennials. Morphology suggests a close affinity to *O. fruticosa* subsp. *fruticosa*. They both may be derived from a common diploid ancestor or *O. pilosella* may have arisen directly from tetraploid *O. fruticosa* subsp. *fruticosa*, which is occasionally weakly rhizomatous.

Systematic Treatment

Oenothera L. sect. **Kneiffia** (Spach) Endl., Gen. Pl. 1191. 1840.

Kneiffia Spach, Hist. Nat. Vég. Phan. 4: 373. 1835; Pennell, Bull. Torrey Bot. Club 46: 373. 1919.
Oenothera subgen. *Kneiffia* (Spach) Munz, Bull. Torrey Bot. Club 64: 287. 1937.

Annual or perennial, erect to decumbent, caulescent herbs from a ± thickened rootstock. Underground parts fibrous or somewhat fleshy roots, or a taproot, the plants occasionally rhizomatous. Seedling or overwintering basal rosette persistent to or during early flowering. Rosette leaves and lower cauline

leaves largest, decreasing in size upward. Basal leaves spatulate, narrowing to a winged petiole, glabrous to densely pubescent, with ciliate margins; often blotched, streaked, or entirely red or purple, subentire to coarsely dentate, ± undulate; tips acute to mucronate. Cauline leaves alternate, linear to ovate, sessile to ± petiolate. Flowers in axils of cauline leaves or in a ± pedunculate terminal raceme or corymb, not usually sharply delimited; subtended by leafy bracts, spreading laterally to erect. Calyx splitting along one side and ± from the base, reflexed as a unit, or with sepals in 2's or all 4 separate, green often turning pink or red at anthesis. Floral tube cylindrical, gradually enlarging to the point of calyx attachment. Petals yellow, truncate, cleft, or emarginate, strongly veined, opening near sunrise, closing near sunset and usually fading, or reopening for several days. Stamens and style erect. Stamens yellow, the epi-sepalous ones longer. Pollen yellow. Capsule obovoid to clavate, tetragonal to 4-winged, narrowing ± to a sterile stipe. Seeds few to many in each locule, ovoid, minutely verrucose to papillose, not winged or angled, but ± angled from crowding within the capsule. Basic chromosome number, $x = 7$. Self-incompatibility characteristic of 2 of the 5 species.

Type species: *Kneiffia glauca* Spach = *Oenothera fruticosa* L. subsp. *glauca* (Spach) Straley.

Key to Species and Subspecies

a. Floral bracts shorter than subtended ovaries; cauline leaves linear, less than 1 mm wide; petals 3–5(–7) mm long; annual; mature fruits ellipsoid-rhomboid, 4–6 mm long .... 5. *O. linifolia*

aa. Floral bracts longer than subtended ovaries; cauline leaves lanceolate to ovate, more than 1 mm wide; petals 5–30 mm long; perennial or annual; mature fruits clavate to oblong or elliptic, 8–20 mm long.

- b. Plants annual; flowers in the axils of cauline leaves in the upper half to two-thirds of the plant; Arkansas and Oklahoma to eastern Texas and Alabama .... 4. *O. spachiana*
- bb. Plants perennial; flowers in terminal corymbs or racemes; of wide eastern North American distribution.
  - c. Stigma and anthers held at the same level at anthesis, the anthers shedding pollen directly on the stigma; petals 5–10 mm long; inflorescence usually nodding .... 3. *O. perennis*
  - cc. Stigma held above the anthers at anthesis; petals 15–30 mm long; tip of the inflorescence usually erect.
    - d. Capsules clavate to oblong; free sepal tips usually 1 mm long or less.
      - e. Capsules clavate, widest above the middle; hairs of the ovary and capsule predominately nonglandular; leaves generally pubescent, subentire .... 1a. *O. fruticosa* subsp. *fruticosa*
      - ee. Capsules oblong, widest about the middle; hairs of the ovary and capsule predominately glandular, or the ovary glabrous; leaves subglabrous or sparsely pubescent, ± dentate .... 1b. *O. fruticosa* subsp. *glauca*
    - dd. Capsules narrowly clavate to elliptic; free sepal tips 1–4 mm long.
      - f. Pubescence of erect hairs 1–2 mm long throughout, the plants rarely glabrous; ovary 9–12 mm long; sepal tips divergent; Ohio to Iowa, south to Alabama and Louisiana 2a. *O. pilosella* subsp. *pilosella*
      - ff. Pubescence of densely appressed hairs less than 1 mm long throughout; ovary 4.5–6.5 mm long; sepal tips connivent; prairies of eastern Arkansas, western Louisiana, and eastern Texas .... 2b. *O. pilosella* subsp. *sessilis*

Subsection I. EUKNEIFFIA

Oenothera sect. **Kneiffia** subsect. **Eukneiffia** (Munz) Straley, comb. nov. Based on *Oenothera* subgen. *Kneiffia* (Spach) Munz sect. *Eukneiffia* Munz, Bull. Torrey Bot. Club 64: 288. 1937.

Blennoderma Spach, Nouv. Ann. Mus. Hist. Nat. 4: 406. 1835. TYPE: *B. drummondii* Spach = *Oenothera spachiana* Torr. & A. Gray.
Oenothera sect. *Blennoderma* (Spach) Endl., Gen. Pl. 1191. 1840.
Oenothera subg. *Kneiffia* sect. *Kneiffia* Munz, N. Amer. Fl., ser. 2, 5: 86. 1965.

Erect annual or perennial herbs from a taproot or fibrous rootstock. Stems villous, hirsute, strigose, or glandular-pubescent. Basal leaves ovate to obovate, petiolate; cauline leaves broadly linear to broadly ovate. Inflorescences erect or nodding, or the flowers in the axils of cauline leaves; bracts longer than the subtending ovaries. Sepal tips free. Stigma held above or surrounded by anthers at maturity, the lobes linear. Flowers usually not cleistogamous. Fruits oblanceolate, obovate, or clavate, tetragonal or 4-winged, narrowed ± into a sterile stipe. Gametic chromosome numbers, $n = 7$, 14, 21, 28. Self-incompatibility present in 2 of the 4 species, autogamy or cleistogamy in the others.

Type species: *Kneiffia glauca* Spach = *Oenothera fruticosa* L. subsp. *glauca* (Michx.) Straley.

1. **Oenothera fruticosa** L., Sp. Pl. 346. 1753.

Perennial herbs from fibrous or occasionally somewhat fleshy rootstock. Stems unbranched, or with several branches from the base or more often many branched above, strictly erect, (1–)3–8(–12) dm tall, to decumbent with ascending tips. Vestiture of erect hairs, especially on the upper stems and inflorescences, to densely strigose, glandular-pubescent, a mixture of these types, or subglabrous throughout. Basal leaves, usually withered by anthesis, oblanceolate to obovate, 3–12 cm long, 0.5–3 cm wide, the petiole 1–4 cm long; principal cauline leaves 2–6(–11) cm long, 0.2–2(–5) cm wide, very narrowly elliptic to ovate, usually lanceolate to oblanceolate, subglabrous with ciliate margins and few hairs along the midrib, to densely strigose or velutinous, subentire to coarsely serrate, ± undulate, sometimes glaucous, especially beneath, the petiole 0.1–2(–6) cm long. Inflorescence erect, rarely nodding; subtending bracts ¼ to nearly the length of the flower, linear to lanceolate, 5–40 mm long, 1–10 mm wide. Ovary 3–15(–18) mm long, 1–3 mm thick. Floral tube 5–20 mm long. Sepals 5–20(–22) mm long, 2–3 mm wide, the tips free, connivent or divergent, 0.5–1(–6) mm long. Petals (8–)15–25(–30) mm long, (6–)10–20(–30) mm wide, truncate to cleft, often undulate, pale to dark yellow. Filaments 5–15 mm long, erect; anthers 4–7 mm long; pollen 130–140 μm in diameter. Style 12–20 mm long, held above the anthers at anthesis; stigmatic lobes 3–5 mm long, divergent. Fruit tetragonal to 4-winged, clavate to oblong, (5–)10–17(–20) mm long, (2–)3–4(–6) mm thick, gradually or abruptly narrowed to a distinctive stipe 1–10 mm long. Seeds dark reddish brown, ca. 1 mm long, ca. 0.5 mm thick, papillose. Self-incompatible. Gametic chromosome numbers, $n = 14$, 21.

Distribution (Figs. 78–79): Forming mostly distinct populations in a wide variety of open habitats, largely in partially stabilized, previously disturbed places, from the Gaspé Peninsula of Quebec and western Nova Scotia westward to northern Michigan and south throughout much of the eastern United States to northcentral Florida and eastern Oklahoma.

Illustration: Gleason (1963: 595).

Oenothera fruticosa consists of two subspecies which at their geographical and morphological extremes are quite distinct, but with many populations and individual plants that are morphologically transitional with much overlapping variation. *Oenothera fruticosa* subsp. *fruticosa* has a more southern distribution and at higher latitudes is more commonly found at lower elevations. In contrast, *O. fruticosa* subsp. *glauca* has a more northern distribution and is most distinctive morphologically in the high southern Appalachians. There is a broad zone of geographical overlap of the two subspecies where there is also much overlap in morphological characters, especially in central Pennsylvania to Virginia, Ohio, Kentucky, and Tennessee.

1a. **Oenothera fruticosa** L. subsp. **fruticosa**.

Oenothera florida Salisb., Prodr. Stirp. 278. 1796, illeg. subst. Based on *O. fruticosa* L.

O. linearis Michx., Fl. Bor. Amer. 1: 225. 1803. LECTOTYPE: North Carolina, *A. Michaux* (P, photograph GH; P, isolectotype).

O. riparia Nutt., Gen. N. Amer. Pl. 1: 247. 1818. TYPE: North Carolina, New Hanover Co., Wilmington, banks of the Cape Fear River, *T. Nuttall* (PH).

Kneiffia suffruticosa Spach, Hist. Nat. Vég. Phan. 4: 367. 1835, illeg. subst. Based on *Oenothera fruticosa* L.

K. linearis (Michx.) Spach, Hist. Nat. Vég. Phan. 4: 367. 1835.

K. angustifolia Spach, Nouv. Ann. Mus. Hist. Nat. 4: 367. 1835, illeg. subst. Based on *Oenothera linearis* Michx.

Oenothera fruticosa L. var. *vera* Hook., Bot. Mag. 64: sub. *pl. 3545.* 1837.

O. fruticosa L. var. *linearifolia* Hook., Bot. Mag. 64: sub. *pl. 3545.* 1837. TYPE: (K, not seen).

O. fruticosa L. var. *linearis* (Michx.) S. Wats., Proc. Amer. Acad. Arts 8: 584. 1873.

O. fruticosa L. var *humifusa* Allen, Bull. Torrey Bot. Club 1: 3. 1879. LECTOTYPE: New York, Suffolk Co., Montauk Point, July 1869, *T. F. Allen* (NY; GH, MICH, isolectotypes); Pennell, Bull. Torrey Bot. Club 46: 368. 1919.

Kneiffia fruticosa (L.) Spach ex Raimann, in Engl. & Prantl, Nat. Pflanzenfam. III, 7: 214. 1893.

Oenothera linearis Michx. var. *alleni* Britton, Mem. Torrey Bot. Club 5: 235. 1894, nom. illeg. Based on *O. fruticosa* L. var. *humifusa* Allen.

Kneiffia longipedicellata Small, Bull. Torrey Bot. Club 23: 178. 1896. LECTOTYPE: Virginia, Albemarle Co., 21 May 1889, *W. C. Rives* (NY); Pennell, Bull. Torrey Bot. Club 46: 368. 1919.

K. subglobosa Small, Bull. Torrey Bot. Club 23: 177. 1896. LECTOTYPE: Georgia, DeKalb Co., Stone Mountain, 6–12 Sep. 1894, *J. K. Small* (NY; MO, US, isolectotypes); Pennell, Bull. Torrey Bot. Club 46: 367. 1919.

K. alleni (Britton) Small, Bull. Torrey Bot. Club 23: 177. 1896.

Onothera fruticosa L. f. *angustifolia* H. Lév., Monogr. Onoth. 108. 1902. No type designated; Munz, Bull. Torrey Bot. Club 64: 293. 1937.

O. fruticosa L. var. *angustifolia* (Spach) H. Lév., Monogr. Onoth., opposite p. 108. 1902.

O. fruticosa L. f. *diversifolia* H. Lév., Monogr. Onoth. 108. 1902. TYPE: Alabama, Lee Co., 8 May 1897, *T. S. Earle & C. F. Baker* (MO-91314, holotype; F, NY, isotypes).

Kneiffia arenicola Small, Fl. S.E. U.S. 842, 1135. 1903. TYPE: Georgia, Richmond Co., Augusta, 27 July 1900, *Biltmore Herb. 5649d* (NY).

Oenothera longipedicellata (Small) B. L. Robinson, Rhodora 10: 34. 1908.

O. linearis Michx. var. *camesii* B. L. Robinson, Rhodora 10: 34. 1908. TYPE: Connecticut,

Fairfield Co., Stratford, sandy shores of Fresh Pond (salt water), 30 Aug. 1896, *E. Eames* (GH).

O. fruticosa L. var. *eamesii* (B. L. Robinson) Blake, Rhodora 20: 51. 1918.

Kneiffia fruticosa L. var. *humifusa* (Allen) Pennell, Bull. Torrey Bot. Club 46: 368. 1919.

K. semiglandulosa Pennell, Bull. Torrey Bot. Club 46: 369. 1919. TYPE: Mississippi, Harrison Co., Biloxi, 21 Apr. 1898, *S. Tracy 5064* (US, holotype; F, MICH, MO, MSC, NY, OSU, isotypes).

K. brevistipata Pennell, Bull. Torrey Bot. Club 46: 369. 1919. TYPE: Mississippi, Pearl River Co., Poplarville, 7 July 1891, *S. Tracy 1681* (US).

K. velutina Pennell, Bull. Torrey Bot. Club 46: 370. 1919. TYPE: New York, Suffolk Co., Garden City, 23 June 1902, *F. A. Mulford* (NY).

K. tetragona Roth var. *longistipata* Pennell, Bull. Torrey Bot. Club 46: 371. 1919. TYPE: South Carolina, Pickens Co., woods near Clemson, 12 May 1907, *H. D. House 3340* (NY).

K. charlesii Lahman, Proc. Oklahoma Acad. Sci. 11: 35. 1931. TYPE: Oklahoma, Delaware Co., between Paule Valley and Davis, dry soil, *M. S. Lahman* (not located).

Oenothera subglobosa (Small) Weatherby & Griscom, Rhodora 36: 48. 1934.

O. subglobosa Small var. *arenicola* (Small) Weatherby & Griscom, Rhodora 36: 48. 1934.

O. fruticosa L. var. *subglobosa* (Small) Munz, Bull. Torrey Bot. Club 64: 295. 1937.

O. tetragona Roth var. *longistipata* (Pennell) Munz, Bull. Torrey Bot. Club 64: 298. 1937.

O. tetragona Roth var. *velutina* (Pennell) Munz, Bull. Torrey Bot. Club 64: 299. 1937.

O. tetragona Roth var. *brevistipata* (Pennell) Munz, Bull. Torrey Bot. Club 64: 301. 1937.

O. tetragona Roth var. *riparia* (Nutt.) Munz, Bull. Torrey Bot. Club 64: 302. 1937.

O. fruticosa L. var. *microcarpa* Fernald, Rhodora 41: 550, *tab. 576, figs. 1–2.* 1939. TYPE: Virginia, Prince George Co., argillaceous and siliceous boggy depressions about 3 mi southeast of Petersburg, on headwaters of Blackwater River, 25 June 1936, *M. L. Fernald, B. Long & R. F. Smart 5860* (GH, holotype; NY, isotype).

O. fruticosa L. var. *unguiculata* Fernald, Rhodora 41: 551, *tab. 577, figs. 1–3.* 1939. TYPE: Virginia, Greensville Co., dry pine woods south of Skippers, 21 May 1939, *M. L. Fernald & B. Long 9991* (GH, holotype; DUKE, MO, NY, PH, POM, US, isotypes).

O. fruticosa L. var. *goodmanii* Munz, N. Amer. Fl., ser. 2, 5: 89. 1965. TYPE: Oklahoma, Latimer Co., Robber's Cave State Park, 6 May 1961, *G. Goodman 7101* (RSA-145160, holotype; GH, isotype).

O. tetragona Roth subsp. *tetragona* var. *sharpii* Munz, N. Amer. Fl., ser. 2, 5: 91. 1965. TYPE: Tennessee, Coffee Co., wet oak barrens with prairie openings, 4 mi southeast of Manchester, 4 July 1947, *A. Sharp, A. Clebsch & E. Clebsch 4830* (RSA-48269).

O. tetragona Roth subsp. *glauca* var. *riparia* (Nutt.) Munz, N. Amer. Fl., ser. 2, 5: 92. 1965.

Kneiffia fruticosa L. var. *unguiculata* (Fernald) Moldenke, Phytologia 31: 373. 1975.

Perennial herbs from fibrous or somewhat fleshy rootstock. Stems (1–)3–8(–12) dm tall, simple or with several branches from the base, or many ± ascending branches above, strictly erect to decumbent with ascending tips. Vestiture of erect hairs especially on the upper stems and inflorescence to densely strigose, or rarely glandular pubescent. Basal leaves oblanceolate to obovate, 3–10 cm long, 0.5–2 cm wide, the petiole 1–4 cm long; cauline leaves 2–6(–8) cm long, 0.2–1.5(–2) cm wide, narrowly elliptic to narrowly ovate, subglabrous to densely strigose or velutinose, mostly subentire, the petiole 0.2–2(–4) cm long. Inflorescence erect or rarely nodding; subtending bracts linear to lanceolate, 5–40 mm long, 1–2(–3) mm wide. Ovary clavate to narrowly oblong, (6–)10–15(–18) mm long, 1–2 mm wide, sparsely to densely hirsute, strigose, or occasionally glabrous, or with a few glandular hairs. Floral tube 5–15 mm long. Sepals 5–20 mm long, 2–3 mm wide, the tips free, usually connivent, 0.5–1(–6) mm long. Petals (8–)15–25 mm long, (6–)10–20(–25) mm wide, truncate to cleft. Filaments 5–15 mm long; anthers 4–6 mm long; pollen 130 μm in diameter. Style 12–18 mm long; stigmatic lobes 3–4 mm long. Capsule tetragonal (rarely 4-winged), clavate to oblong-clavate, (5–)10–17(–20) mm long, (2–)3–4 mm thick, widest above the

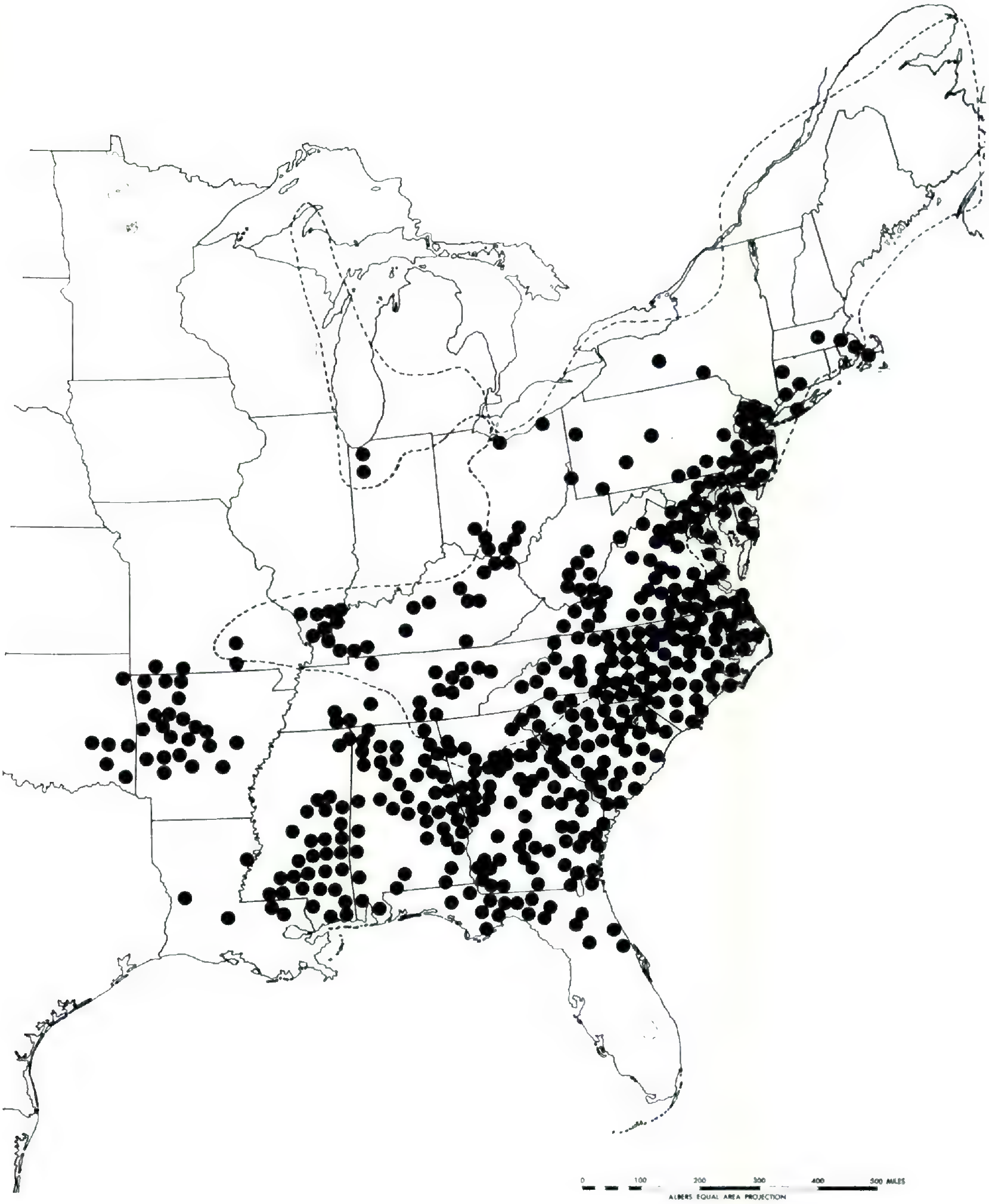


FIGURE 78. Distribution of *Oenothera fruticosa* subsp. *fruticosa*. The dotted line shows the distribution of *O. fruticosa* subsp. *glauca*.

middle, gradually narrowed into a stipe 3–10 mm long. Gametic chromosome numbers, $n = 14, 21$. Self-incompatible.

Type: Sheet 484-8 (LINN; photograph, POM) without definite locality, *P. Kalm*. The Clayton specimens in the Gronovius herbarium (BM) discussed by Blake (1918: 50–52) should not be taken as types of this entity, since Linnaeus's description was clearly based on material he had on hand at the time he was preparing it. Pennell (1919) and Munz (1937) were therefore in error in con-

sidering "*Clayton 36*" (BM) as the type of this species. Linnaeus's phrase "Habitat in Virginia," however, must refer to the Gronovius reference.

Distribution (Fig. 78): Frequent in meadows, open woods and woods' edges, margins of salt and freshwater marshes, stabilized sand dunes, roadsides, and other partially disturbed habitats, from coastal Massachusetts to northern Florida, westward to northern Indiana, eastern Oklahoma and Louisiana.

The complex synonymy of *O. fruticosa* subsp. *fruticosa* reflects the variability of this taxon. The following are particularly variable characters:

1. *Habit*: Toward the southern and western portion of the distribution—i.e., coastal Georgia and Florida to Arkansas and Oklahoma—plants in most populations are relatively short (1.5–3 dm tall) and mostly unbranched with relatively large flowers (petals to 2 cm long). The basal rosette of leaves often remains green during early flowering. Toward the northern portions of the range—i.e., central Virginia to Massachusetts and westward to Ohio and Michigan, as well as in the highlands of the South—most populations tend to be taller (to 10 dm) and more branched from the base or higher on the plants. The flowers are often smaller (petals to 1.5 cm long). Very robust plants (to 12 dm tall) from coastal North and South Carolina, recognized as *O. riparia* Nutt., are quite distinct at their extremes, but there are many intermediate individuals and populations between these and more typical populations of *O. fruticosa* subsp. *fruticosa*. These most robust plants do deserve further study, especially cytologically, however. Other populations, particularly from the edges of salt marshes and sand dunes along the Atlantic Coast, are low growing (1.5–2 dm tall and equally broad) and much branched at the base and above, and have been known as *O. fruticosa* var. *humifusa* Allen and *O. linearis* var. *eamesii* B. L. Robinson. Collections typical of these include: Fairfield Co., CT, 7 Aug. 1878, *Eames* (GH); Suffolk Co., NY, *Barnhart 1135* (NY, VT); and Sussex Co., DE, *McVaugh 6519* (GH). There are many intergradations into typical *O. fruticosa* subsp. *fruticosa* in areas away from the salt marshes and in less sandy areas, as noted by Allen (1870). This variability in habit seems to be directly related to environmental factors. Somewhat similar populations from serpentine barrens of southeastern Pennsylvania and central Maryland, as in Chester Co., PA, *Straley 844* (MO) and Cecil Co., MD, *Long 28387* (GH) are often intermediate in height and branching between those along the coast and those more typical of *O. fruticosa* subsp. *fruticosa*. Many populations in southern Illinois, adjacent Kentucky, and parts of Michigan, Indiana, and Ohio consist of much-branched individuals with very narrow leaves, and many branches which are held quite erect high on the plant. Branching may also be a seasonally variable character as demonstrated in collections from Sussex Co., VA, *Straley 877* (MO) which early in the season (May, June) at initial flowering consist of plants with unbranched stems, but later these become much branched. Grazing, mowing, or other mechanical damage to the primary apex may also stimulate branching as shown in collections from Northampton Co., NC, *Straley 884* (MO), which in nature had simple stems, but under cultivation became much branched.

This taxon apparently becomes rhizomatous at times in dry oak woods as in

collections from Conway Co., AR, *Straley 861* (MO) and Faulkner Co., AR, *Straley 866* (MO) which in nature produced rhizomes 3–5 cm long. This, however, seems again to be an ecological response, because the following year under moister greenhouse conditions and the second year in the experimental garden, the same plants produced no rhizomes, the basal rosettes being produced directly from the base of the current year's rootstock.

2. *Pubescence*: Although the plants tend to be pubescent throughout, there is great variability in the amount and type of pubescence. In general the most pubescent populations are in the southern and especially in the western parts of the distribution. The hairs may be erect and long (1 to nearly 2 mm), then approaching the pubescence of *O. pilosella* subsp. *pilosella* or, more frequently, sparsely to densely strigose with hairs about 1 mm long or less. Collections with especially dense strigose pubescence are, among others, Suffolk Co., NY, *Barnhart 2806* (NH), Coffee Co., TN, *Straley 957* (MO), and one collection with unusually long strigose pubescence is from Durham Co., NC, *Luteyn 3411* (DUKE). The absence of glandular hairs on the inflorescence has in the past been used as a primary characteristic of this taxon. There are, however, many individuals from throughout its range with at least a few glandular hairs, although they otherwise have all the typical characters of *O. fruticosa* subsp. *fruticosa*. Glandular hairs become more frequent toward the northern part of the range and at higher elevations, but there normally remains a predominance of nonglandular hairs over glandular ones. The presence of glandular hairs seems to be more prevalent early in the season, and during wet weather, while the same plant will have predominately nonglandular hairs later in the season or during extended dry weather. This has been demonstrated with the Sussex Co., VA, population *Straley 884* (MO) in the growth chamber and experimental garden. The variation in pubescence type can be seen from plant to plant within a population, ranging from completely glabrous to entirely glandular, entirely nonglandular, or a mixture of both as in collections from Coffee Co., TN, *Kral 26861* (TENN, VDB).

3. *Leaves*: The leaves are quite variable in size, shape (Figs. 1–10), and pubescence in individual plants as well as between populations. There is a general trend toward broader leaves from the southern and western part of the range toward the northern and central portions and at higher elevations. Leaf size and shape may also change with the maturity of the plant. Early in the season the primary cauline leaves are usually very narrowly elliptic or narrowly oblanceolate, but by midsummer these primary leaves will usually have fallen and the leaves on the secondary branches will be elliptic to obovate, giving the plant an entirely different aspect. Among those collections with unusually broadly elliptic to obovate leaves are collections from central Tennessee to northern Alabama and Mississippi as in Coffee Co., TN, *Blum 3673A* (VDB, FSU, OS) and Jones Co., MS, *Teer 62* (SMU) which bear cauline leaves much more the shape of, although generally smaller, those typical of *O. fruticosa* subsp. *glauca*. The margins of the leaves in this taxon are usually subentire with some populations or individual plants with subdentate margins, and some occasionally with undulate margins.

4. *Inflorescence*: Nodding inflorescence tips are characteristic of *O. perennis* but are usually absent from the other perennial species. In a few populations of *O. fruticosa* subsp. *fruticosa*, however—e.g., those from Northampton Co., NC, *Straley 877* (MO) and Baltimore Co., MD, *Straley 886* (MO)—the tips of the inflorescence are nodding.

5. *Flowers*: Many-flowered racemes are most common in populations in the north and few-flowered racemes or cymes are more common in the southern part of the range. Flowering may continue gradually over a period of two months or more, or may last only a week or two, especially in the few-flowered populations with cymose inflorescences.

6. *Sepals*: Although sepal tips are usually about 1 mm long, populations along the coast of southern North Carolina and adjacent South Carolina frequently include individuals with much longer sepal tips (to 6 mm long) which are usually quite divergent.

7. *Capsules* (Figs. 40–41, 44): One of the most variable characters in this subspecies is the size, shape, and pubescence of the capsule. They are usually distinctly clavate, widest above the middle, and with a straight or incurved stipe, but may be subsessile. The body of the capsule may be globose and quite small (3–4 mm long, 2–3 mm thick) with a relatively long stipe (4–6 mm long) as in the collections from Prince George Co., VA, *Fernald, Long & Smart 5860* (GH) described as var. *microcarpa* Fern. Very large capsules (to 22 mm long and 5 mm thick) occur in populations along the coast of the Carolinas. In other populations, the capsules may be subsessile as in plants from Gateswood, AL, *Tracy 8497* (F), to quite stipitate with a stipe 15–20 mm long as in Macon Co., AL, *Kral 46106* (VDB) and Orange Co., NC, 20 May 1939, *Martin & Stewart* (NCU, NY).

Numerous individuals and populations which are intermediate in one or several morphological characters between this taxon and *O. fruticosa* subsp. *glauca* will be discussed under that taxon.

Oenothera fruticosa subsp. *fruticosa* has been previously reported as tetraploid ($n = 14$) by Linder (1954) without reference to origin of the population, by Gregory & Klein (1960) from Mecklenburg Co., NC, *Munz & Gregory 23497* (RSA), and by Laws (1963) from Jackson Co., NC (no voucher), with rings of 4 chromosomes at metaphase I. Another Gregory & Klein (1960) report from Hardin Co., TN, *Munz & Gregory 23500* (RSA) of tetraploid *O. tetragona* Roth var. *brevistipata* (Pennell) Munz is also referable to *O. fruticosa* subsp. *fruticosa*. Laws (1963) also reports six hexaploid ($n = 21$) populations from Durham Co., NC, June 1961, *Laws* (DUKE) with variable meiotic associations of up to 7 rings of 6. Another hexaploid population from Jasper Co., SC, *Munz & Gregory 23491* (RSA) was reported by Gregory & Klein (1960) as *O. tetragona* Roth var. *tetragona*. The meiotic configuration reported was: 1 ring of 6, 1 chain of 6, 4 rings of 4, 1 chain of 4, and 5 pairs.

Vouchers for chromosome number (39 individuals, 22 populations): Tetraploid, $n = 14$. ALABAMA: Barbour Co., *Straley 900*, 1 ring of 4, 10 pairs. Chambers Co., *Straley 890*, *Straley 893*, 2 rings of 4, 10 pairs. Lee Co., *Straley 894*. Randolph Co., *Straley 889*. ARKANSAS: Conway Co., *Straley 861*. Faulkner Co., *Straley 866*. GEORGIA: Jenkins Co., *Straley 920*. Tattnall Co., *Straley 919*. FLORIDA: Gadsden Co., *Straley 914*. Jackson Co., *Straley 901*, *904*.

MARYLAND: Baltimore Co., *Straley 886.* TENNESSEE: Coffee Co., *Straley 957.* VIRGINIA: Amelia Co., *Straley 1078.* Bland Co., *Straley 754.* Carroll Co., *Straley 747, 748.* Dinwiddie Co., *Straley 707.* Nottoway Co., *Straley 1072.* Prince George Co., *Straley 1076.* Sussex Co., *Straley 982.* WEST VIRGINIA: Monroe Co., *Straley 713,* 3 rings of 4, 8 pairs.

Vouchers for chromosome number (17 individuals, 7 populations): Hexaploid, $n = 21$. FLORIDA: Wakulla Co., *Straley 915, 916.* NORTH CAROLINA: Northampton Co., *Straley 884.* VIRGINIA: Prince Edward Co., *Straley 1075.* Sussex Co., *Straley 877,* 3 rings of 6, 1 chain of 6, 3 rings of 4, 3 pairs; *Straley 1087.* Virginia Beach, *Straley 701,* 1 chain of 6, 3 rings of 4, 1 chain of 4, 10 pairs.

1b. **Oenothera fruticosa** L. subsp. **glauca** (Michx.) Straley, comb. nov. Based on *Oenothera glauca* Michx., Fl. Bor. Amer. 1: 224. 1803.

O. tetragona Roth, Catalecta Bot. 2: 39. 1800. TYPE: Grown in the garden of Wilhelm Koch, at Gnadau, near Barby, Germany, of American origin.
O. hybrida Michx., Fl. Bor. Amer. 1: 225. 1803. LECTOTYPE: North Carolina, *A. Michaux* (P, photograph GH; P, isolectotype); Munz, Bull. Torrey Bot. Club 64: 301. 1937.
O. fraseri Pursh, Fl. Amer. Sept. 2: 734. 1814. TYPE: Cultivated plants grown from seed collected in South Carolina by Fraser.
O. fruticosa L. var. *ambigua* Nutt., Gen. N. Amer. Pl. 1: 247. 1818. TYPE: Common around Philadelphia (BM, not seen).
O. incana Nutt., Gen. N. Amer. Pl. 1: 247. 1818. TYPE: Maryland, dry woods, *W. C. Barton* (PH).
O. canadensis Goldie, Edinburgh Philos. J. 6: 325. 1822. LECTOTYPE: Canada, Quebec, Island of Montreal, spring 1819, *J. Goldie* (K, not seen); Munz, Bull. Torrey Bot. Club 64: 298. 1937.
O. ambigua (Nutt.) Spreng., Syst. Veg. 2: 229. 1825.
O. serotina Lehm., Ind. Sem. Hort. Hamb. 1825: 17. 1825.
O. serotina Sweet, Brit. Fl. Gard. I, 2: *pl. 184.* 1826. TYPE: From the Botanical Garden at Liverpool, original source not known.
Kneiffia glauca (Michx.) Spach, Hist. Nat. Vég. Phan. 4: 374. 1835.
K. fraseri (Pursh) Spach, Hist. Nat. Vég. Phan. 4: 375. 1835.
K. floribunda Spach, Hist. Nat. Vég. Phan. 4: 376. 1835, illeg. subst. Based on *Oenothera tetragona* Roth.
K. maculata Spach, Hist. Nat. Vég. Phan. 4: 375. 1835, illeg. subst. Based on *Oenothera serotina* Sweet.
Oenothera fruticosa L. var. *fraseri* (Pursh) Hook., Bot. Mag. 64: sub *pl. 3545.* 1837.
O. fruticosa L. var. *incana* (Nutt.) Hook., Bot. Mag. 64: sub *pl. 3545.* 1837.
O. fruticosa L. var. *indica* Lindley, Bot. Reg. 27: *pl. 11.* 1841. LECTOTYPE: Bot. Reg. 27: *pl. 11.* 1841, grown in the Garden of the Horticultural Society in London, from seeds given to the Society by Dr. Royle, said to have been collected in Kashmir, India; Munz (1937: 299) saw a specimen of the probable type "Garden, July 1839, d. Lindley" (B). Destroyed during World War II.
O. glauca var. *fraseri* (Pursh) Walp., Repert. Bot. Syst. 2: 84. 1843.
O. fruticosa L. var. *differta* Millspaugh, Fl. W. Va. 366. 1892. LECTOTYPE: West Virginia, Wood Co., Kanawha Station, roadside, 1 July 1890, *C. Millspaugh* (WVA, not seen, photograph POM; NY, isolectotype); Munz, Bull. Torrey Bot. Club 64: 294. 1937.
Onothera fruticosa L. var. *glauca* (Michx.) H. Lév., Monogr. Onoth. 107. 1902.
O. fruticosa L. f. *lucida* H. Lév., Monogr. Onoth. 108. 1902. TYPE: Cultivated in the Valleyres Garden, Switzerland, *Herb. Boissier* (G, not seen).
O. fruticosa L. var. *maculata* H. Lév., Monogr. Onoth. 107. 1902.
Kneiffia fruticosa L. var. *differta* (Millspaugh) Millspaugh, Living Fl. W. Va. 312. 1913.
Oenothera hybrida Michx. var. *ambigua* (Nutt.) S. F. Blake, Rhodora 20: 52. 1918.
Kneiffia tetragona Roth var. *hybrida* (Michx.) Pennell, Bull. Torrey Bot. Club 46: 371. 1919.
K. latifolia Rydb., Torreya 27: 86. 1927. TYPE: North Carolina, Buncombe Co., Craggy Mountains, 21 July 1925, *P. A. Rydberg 9455* (NY).
Oenothera tetragona Roth var. *fraseri* (Pursh) Munz, Bull. Torrey Bot. Club 64: 300. 1937.
O. tetragona Roth var. *fraseri* Pursh f. *hybrida* (Michx.) Munz, Bull. Torrey Bot. Club 64: 300. 1937.

O. tetragona Roth var. *fraseri* Pursh f. *latifolia* (Rydb.) Munz, Bull. Torrey Bot. Club 64: 301. 1937.
O. tetragona Roth subsp. *glauca* (Michx.) Munz, N. Amer. Fl., ser. 2, 5: 91. 1965.

Perennial herbs from fibrous rootstock. Stems simple or branched at the base or with spreading to ascending branches from above, 2–8(–10) dm tall, strictly erect or slightly decumbent. Vestiture usually sparse, usually of glandular, erect hairs, strigose, or subglabrous. Basal leaves oblanceolate to obovate, 3–12 cm long, 0.5–3 cm wide, the petiole 1–3 cm long; cauline leaves 2–6(–11) cm long, 0.2–2(–5) cm wide, narrowly elliptic to broadly ovate, usually glabrous to sparsely pubescent, subentire to coarsely dentate, undulate, the petiole 0.1–2 (–6) cm long, sometimes glaucous, especially below. Inflorescence erect; subtending bracts linear to ovate, 5–40 mm long, 1–10 mm wide. Ovary narrowly to broadly obovoid, (3–)4–8(–13) mm long, 1–3 mm thick, sparsely to densely covered with glandular hairs and sometimes also with nonglandular erect hairs, or strigose. Floral tube 5–20 mm long. Sepals 8–22 mm long, 2–3 mm wide, the tips free, connivent to divergent. Petals (8–)15–20(–30) mm long, (6–)10–20(–30) mm wide, truncate to cleft. Filaments 5–15 mm long; anthers 4–7 mm long; pollen ca. 140 μm in diameter. Style 12–20 mm long; stigmatic lobes 3–5 mm long. Capsule tetragonal to 4-winged, oblong to oblong-clavate, widest at the middle, (5–)10–17(–20) mm long, (2–)3–4(–6) mm thick, usually abruptly tapered to a stipe 0.1–3(–7) mm long. Gametic chromosome number, $n = 14$. Self-incompatible.

Type: "Hab. in silvis remotis et occidentalibus flumini *Mississippi* confinibus, versus regioneum Illinoensium." The specimen (P, photograph GH; P, isotype) is labeled "Ouest de Ohio, Route aux Illinois," but the plant is presumably from the southern Appalachians, in the Carolinas or Virginia where he collected in June and July of 1787 and 1789; Sargent (1889), Thwaites (1904), Pennell (1919: 371).

Distribution (Fig. 79): Open meadows, stream margins, and edges of woods, more frequent at higher elevations, locally from the Gaspé Peninsula of Québec, southern Ontario, and western Nova Scotia to northern Michigan, southward through eastern Kentucky and Tennessee, and in the Appalachian Mountains to northern Georgia. Of a more northern and narrower distribution than *O. fruticosa* subsp. *fruticosa.*

Illustration: Gleason (1963: 595) as *O. tetragona* and var. *fraseri.*

The northern natural limits of distribution of this taxon are not clear. It is commonly cultivated in gardens, and Canadian collections as well as a somewhat disjunct population on the northern peninsula of Michigan, Keweenaw Co., *Herman 8041* (MICH, US) may be local escapes, but nevertheless appear to be well established. An old collection from Montréal, Québec, in 1819, collected and named *O. canadensis* by Goldie is apparently a natural population which probably has not survived. One disjunct population, although typical of this taxon, is from southeastern Missouri, Shannon Co., May 1939, *Kellogg 28* (MO), and may represent a Pleistocene relict.

This taxon is by far the most variable in the section. It is most distinctive morphologically in the southern Appalachians, with many intergrading popula-

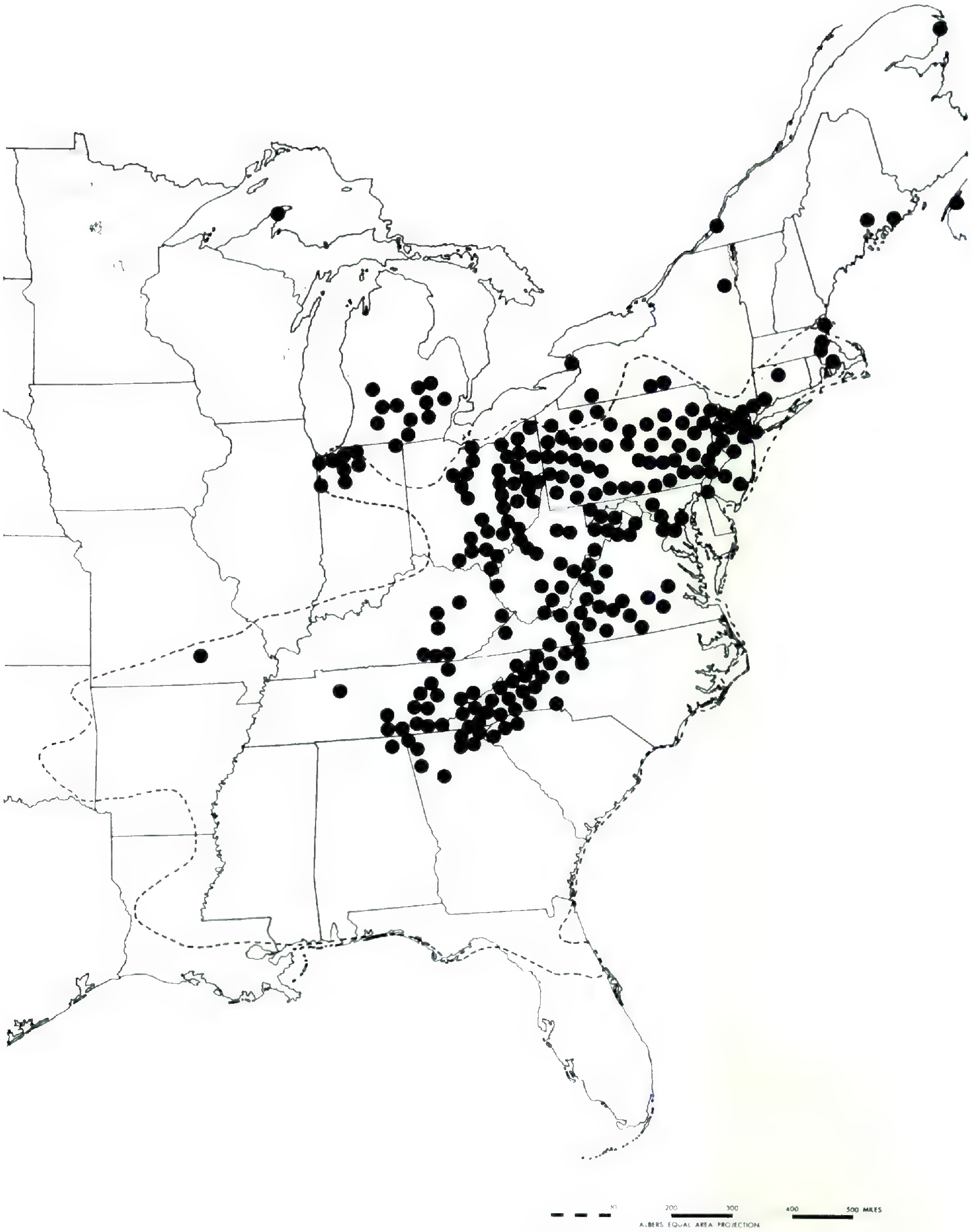


FIGURE 79. Distribution of *Oenothera fruticosa* subsp. *glauca*. The dotted line shows the distribution of *O. fruticosa* subsp. *fruticosa*.

tions with *O. fruticosa* subsp. *fruticosa* at lower elevations. The following are among the most variable characters:

1. *Habit*: Plants may be unbranched to quite branched from the base or higher. In the distinctive high altitude populations of the Appalachians, the branches tend to be few and are held at wide angles. In most other areas the branches are much more erect.

2. *Leaves*: These are extremely variable in size and shape (Figs. 11–20). In plants from the higher Appalachians, the leaves are usually broadly elliptic to broadly ovate, becoming more lanceolate to very narrowly elliptic northward and at lower elevations. Cauline leaves are usually sessile, but they may have petioles up to 6 cm long as in collections from Amelia Co., VA, *Straley 1078*. Leaf margins are usually remotely dentate to subentire. They are typically more dentate than in most populations of *O. fruticosa* subsp. *fruticosa*. Among the collections with coarsely dentate leaves are those from Caldwell Co., NC, *Ahles 43995 & Duke* (NCU) and Rockland Co., NY, *Lehr 886* (NY). Only at the higher elevations of the southern Appalachians do populations have leaves which are quite glaucous, especially beneath and particularly in the populations with the broadest leaves, which was clearly the reason for Michaux naming this taxon *O. glauca*. Many of the glaucous-leaved plants have very thick leathery leaves compared with those of plants from lower altitudes and higher latitudes. Among many examples of these thick, broad-leaved, glaucous collections are those from Patrick Co., VA, *Kral 9262* (VDB) and Pike Co., KY, *McVaugh 8695* (MICH, NA). Other broad-leaved collections are not at all glaucous and have very thin, translucent leaves as in collections from White House, KY, *Biltmore Herb. 6739* (US) and Yancey Co., NC, *Lloyd 4746* (MO).

3. *Pubescence*: Some plants are glabrous throughout, whereas others have strigose inflorescences and leaves, especially along the midrib and margins and stems. Most frequent are plants with short, erect, glandular hairs on the stems and especially the inflorescences. Glandular hairs usually predominate over nonglandular ones, and there are usually more glandular hairs on the young inflorescences early in the season. These apparently fall from the capsules as they mature. A few plants had long erect hairs (to 2 mm) on the stems and leaves, similar to those characteristic of *O. pilosella* subsp. *pilosella*: Watauga Co., NC, 22 June 1891, *Small & Heller* (F, MASS, PH, POM, YALE) and Caldwell Co., NC, 24 June 1893, *Heller* (MSC, PH).

4. *Petals*: These vary in size from 1 cm long in many plants from the north and at lower elevations to 2.5–3 cm long in those from the mountains. These larger flowers are frequently paler yellow than the smaller ones. Petals vary from emarginate to truncate and are often undulate distally.

5. *Capsules* (Figs. 42–43): These are the most variable structures in size, shape, and pubescence. At one extreme they are oblong and subsessile, and at the other extreme they are distinctly clavate and stalked, with all intermediate forms represented in different populations and many variations within populations. They are usually widest near the middle, as measured from the base of the stipe to the distal end of the capsule body. The body varies from narrowly ridged to usually distinctly winged. Capsule shape often changes with maturity. Among some collections with very large and broadly winged capsules (23 mm long, 7 mm wide) are those from Patrick Co., VA, *Kral 9262* (VDB).

There are many individuals and populations which are intermediate between the two subspecies of *O. fruticosa*. No single morphological character should be weighed too heavily in placing a plant in either of the subspecies. For example, nonglandular hairs have been regarded traditionally as a key characteristic of

O. fruticosa subsp. *fruticosa*, whereas, in fact, either subspecies may have glandular hairs, although they are more frequent in *O. fruticosa* subsp. *glauca*. In the southern Appalachians where *O. fruticosa* subsp. *glauca* is most distinct, there are few difficulties in separating it from subsp. *fruticosa*. In much of Tennessee, Kentucky, Ohio, Maryland, West Virginia, and Pennsylvania, however, there are many intermediate populations and individuals, and the subspecific lines become much less distinct. By using a combination of characters, however, most specimens may be assigned to one or the other. In general, *O. fruticosa* subsp. *glauca* has broader, usually relatively glabrous, sometimes glaucous, and more dentate leaves; predominately glandular pubescence; and oblong capsules, widest about the middle. *Oenothera fruticosa* subsp. *fruticosa* usually has narrower, more strigose leaves, with subentire margins; predominately nonglandular hairs; and clavate capsules, widest near the distal end.

Among the populations which are intermediate between the two are: Loudon Co., VA, *Hunneywell 10718* (GH), with variable leaf width on different plants, and broadly winged capsules, widest at the middle, but all strigose, nonglandular pubescence; Jackson Co., OH, 22 June 1968, *Bartley* (OS), with clavate capsules, has two plants with glandular hairs and one with only nonglandular hairs; Grant Co., WV, 31 July 1931, *Core* (NY), with clavate capsules, but with only or predominately glandular pubescence.

For states in which there has been an abundance of specimens of these two taxa collected, as in North Carolina, the pattern of distribution, overlap of characters, and intermediate populations is demonstrated quite well, with typical *O. fruticosa* subsp. *fruticosa* in the eastern part of the state at mostly lower elevations, and *O. fruticosa* subsp. *glauca* only in the western part of the state in the mountains. In other states, such as Kentucky, in which there has been much less collecting, the distribution and overlap of characters is less clear.

These two taxa have not been found growing in close proximity, with the exception of one locality in Amelia Co., VA, *Straley 1078, 1079* (MO), which was observed on 31 May 1975, where the two subspecies grow on opposite sides of a road, a few hundred meters apart. The population of *O. fruticosa* subsp. *fruticosa* was confined to a wet marshy area in the edge of a mixed deciduous woods, whereas that of *O. fruticosa* subsp. *glauca* was in the edge of a dry open meadow. The two were close enough for potential crossing by visiting bees but only the last flowers of subsp. *fruticosa* and the first flowers of subsp. *glauca* were open. At least in these populations, the possibilities of crossing were limited to overlap in flowering time of only a few days. No intermediates were found. Nevertheless, the existence of many intermediate populations elsewhere makes it quite clear that hybridization between these entities is and has been very frequent and that the pattern of intergradation between them is complex and nearly complete.

This taxon has been reported as tetraploid by Schwemmle (1924) and from plants cultivated at Edinburgh Botanical Garden by Hagen (1950). The original source of these collections is not known and no voucher specimens were made. The only other published reports of chromosome number for this taxon refer to *O. fruticosa* subsp. *fruticosa*, as already mentioned in the discussion of

that subspecies. A specimen from Clark Co., Virginia, *Baldwin 5189* (GH), was annotated as a tetraploid by Earlene Atchison.

Vouchers for chromosome number (34 individuals, 12 populations): Tetraploid, $n = 14$. NEW JERSEY: Passaic Co., *Straley 760, 1114.* NORTH CAROLINA: Mitchell Co., *Lloyd 4744*, 4 rings of 4, 1 chain of 4, 4 pairs. Transylvania Co., *Lloyd 4749.* Yancey Co., *Lloyd 4745.* VIRGINIA: Amelia Co., *Straley 1078.* Bedford Co., *Straley 875.* Craig Co., *Straley 716, 720*, 3 rings of 4, 2 chains of 4, 6 pairs. WEST VIRGINIA: Greenbrier Co., *Straley 756, 758*, 5 rings of 4, 4 pairs. CULTIVATED: CANADA: NOVA SCOTIA: Pictou Co., *Straley 1103.* UNITED STATES: PENNSYLVANIA: Chester Co., Longwood Gardens, *Straley 842.*

2. **Oenothera pilosella** Raf., Ann. Nat. 1: 15. 1820.

Perennial herb, ± rhizomatous, from a thickened rootstock. Stem erect, simple or a few spreading to ascending branches above, 2–8 dm tall, densely to sparsely hirsute, the hairs 1–2 mm long, or strigose, the hairs less than 1 mm long on the stems, leaves, especially along the midrib and around the margins, and on the inflorescences, rarely glabrous. Basal leaves oblanceolate to ovate, 4–8 cm long, 2–5 cm wide, the petiole (0.5–)1–3(–4) cm long, entire, withering before flowering; cauline leaves mostly lanceolate, less commonly linear to ovate, 2–10(–13) cm long, 1–2(–4) cm wide, the petiole 0.1–0.5(–2) cm long, subentire to coarsely dentate. Inflorescences terminal, erect, and indistinct. Ovary (4.5–)8–12(–14) mm long, (1–)1.5–2.5(–3.5) mm thick, glabrous to sparsely pubescent with spreading hairs, or strigose, oblong or narrowly oblong, sessile or borne on a stipe 1–2 mm long. Floral tube 1–2.5 cm long. Sepals 10–20 mm long, 2–5 mm wide, with free tips 1–3 mm long, connivent to divergent, ± hirsute or strigose. Petals 1.5–3 cm long, 1.5–2.5 cm wide, obcordate to cleft, dark yellow. Filaments 7–15 mm long; anthers 4–8 mm long; pollen 145–165 μm in diameter. Style 10–20 mm long; stigma held well above the stamens at anthesis; stigmatic lobes linear, 2–5 mm long, divergent. Capsule subsessile or stalked, the stipe (1–)3–5(–9) mm long, linear-clavate to elliptic, glabrous to densely hirsute or strigose, (7–)10–15(–20) mm long, 2–4(–5) mm thick, tetragonal, occasionally winged. Seeds dark reddish brown, ca. 1 mm long, ca. 0.5 mm wide, papillose. Gametic chromosome number, $n = 28$. Self-incompatible.

Distribution (Fig. 80): Open fields, edges of woods, and prairies, usually in somewhat marshy places from southern Ontario to Iowa, southward to northern Alabama and eastern Texas. Frequently cultivated and often escaping and becoming established outside its natural range.

Oenothera pilosella is a variable taxon which has been in the past frequently confused with *O. fruticosa*, but the two are actually sharply distinct. Some individuals or populations have individual morphological characters typical of the other taxon, but when overall morphology is considered, specimens are easily referred to one species or the other.

This taxon consists of two subspecies. The first, *O. pilosella* subsp. *pilosella*, has a relatively broad distribution and is especially common in the Midwest and Mississippi River Valley. The second, *O. pilosella* subsp. *demareei* (*O. sessilis* auct.) has, at present, a very narrow distribution in eastern Arkansas, central Louisiana, and the Gulf Coast of Texas.

Based on overlapping morphological characters, it seems best to regard these two entities as subspecies of a single species. They are exclusively octoploid ($n = 28$), and are the only octoploids known in the genus *Oenothera.*

2a. **Oenothera pilosella** Raf. subsp. **pilosella.**

O. fruticosa L. var. *hirsuta* Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1: 496. 1840. LECTOTYPE: Illinois (NY).

O. fruticosa L. var. *pilosella* (Raf.) Small & Heller, Mem. Torrey Bot. Club 3: 26. 1892.

Kneiffia fruticosa L. var. *pilosella* (Raf.) Britton, Mem. Torrey Bot. Club 5: 234. 1894.

K. pilosella (Raf.) Heller, Cat. N. Amer. Pl., ed. 2, 8. 1900.

Onothera fruticosa L. f. *hirsuta* (Nutt. ex Torr. & A. Gray) H. Lév., Monogr. Onoth. 108. 1902.

Kneiffia sumstinei O. Jennings, Ann. Carnegie Mus. 3: 480. 1903. TYPE: Pennsylvania, Armstrong Co., near Kittanning, upland field, June 1905, *D. Sumstine* (CM, holotype, not seen; NY, isotype).

K. pratensis Small, Fl. S.E. U.S. 842, 1335. 1903. TYPE: Missouri, Jefferson Co., wet places, 11 June 1878, *H. Eggert* (NY, holotype; WIS, isotype).

Oenothera pratensis (Small) B. L. Robinson, Rhodora 10: 34. 1908.

O. pilosella Raf. f. *laevigata* Palmer & Steyermark, Brittonia 10: 116. 1958. TYPE: Missouri, Howell Co., 4 mi south of West Plains, *J. Steyermark 78703* (F-1456282, holotype; GH, MO, isotypes).

Rhizomatous perennial herb, from a thickened base, simple or little branched above, the branches spreading or ascending. Stems 2–8 dm tall, densely to sparsely pubescent with spreading hairs 1–2 mm long throughout, rarely glabrous. Basal leaves oblanceolate to ovate, 4–8 cm long, 2–5 cm wide, the petiole (0.5–)1–3(–4) cm long; cauline leaves lanceolate to ovate, subentire to coarsely dentate, lanceolate to ovate, 3–10(–13) cm long, 1–2(–4) cm wide, abruptly narrowed to the base, subsessile or with a petiole to 0.5(–2) cm long. Ovary (4.5–)9–12(–14) mm long, (1–)1.5–2.5(–3.5) mm wide, glabrous or sparsely to densely pubescent with spreading straight hairs 1–2 mm long, narrowly oblong, sessile or with a stipe 1–2 mm long. Floral tube 1–2.5 cm long. Sepals 10–20 mm long, 2–5 mm wide, the tips 1–3 mm long, usually divergent, hirsute. Petals 1.5–3 cm long, 1.5–2.5 cm wide, obcordate to cleft, dark yellow. Filaments 7–15 mm long; anthers 4–8 mm long; pollen 165 μm in diameter. Style 10–20 mm long; stigmatic lobes linear, 2–5 mm long. Capsule linear-clavate to linear-elliptic (rarely elliptic), (5–)10–15(–28) mm long, 2–4(–5) mm wide, 4-angled to slightly winged. Gametic chromosome number, $n = 28$. Self-incompatible.

Type: Indiana, Vanderburgh Co., near Evansville. Apparently no material of Rafinesque's original gathering has survived.

Distribution (Fig. 80): Isolated colonies in wet meadows, edges of woods and prairies, southern Ontario to southern Wisconsin and southeastern Iowa to northern Alabama and central Louisiana. It is widespread in cultivation in gardens and frequently escapes and becomes naturalized; consequently, the northern and eastern natural limits of this taxon are not clear. Apparently, Wayne Co., West Virginia, along the Ohio River and Erie Co., New York, are the eastern limits and Tuscola Co., Michigan, and Mantiwoc Co., Wisconsin, the northern natural limits. Collections from the Upper Peninsula of Michigan are probably from naturalized populations, although they might represent natural disjunct

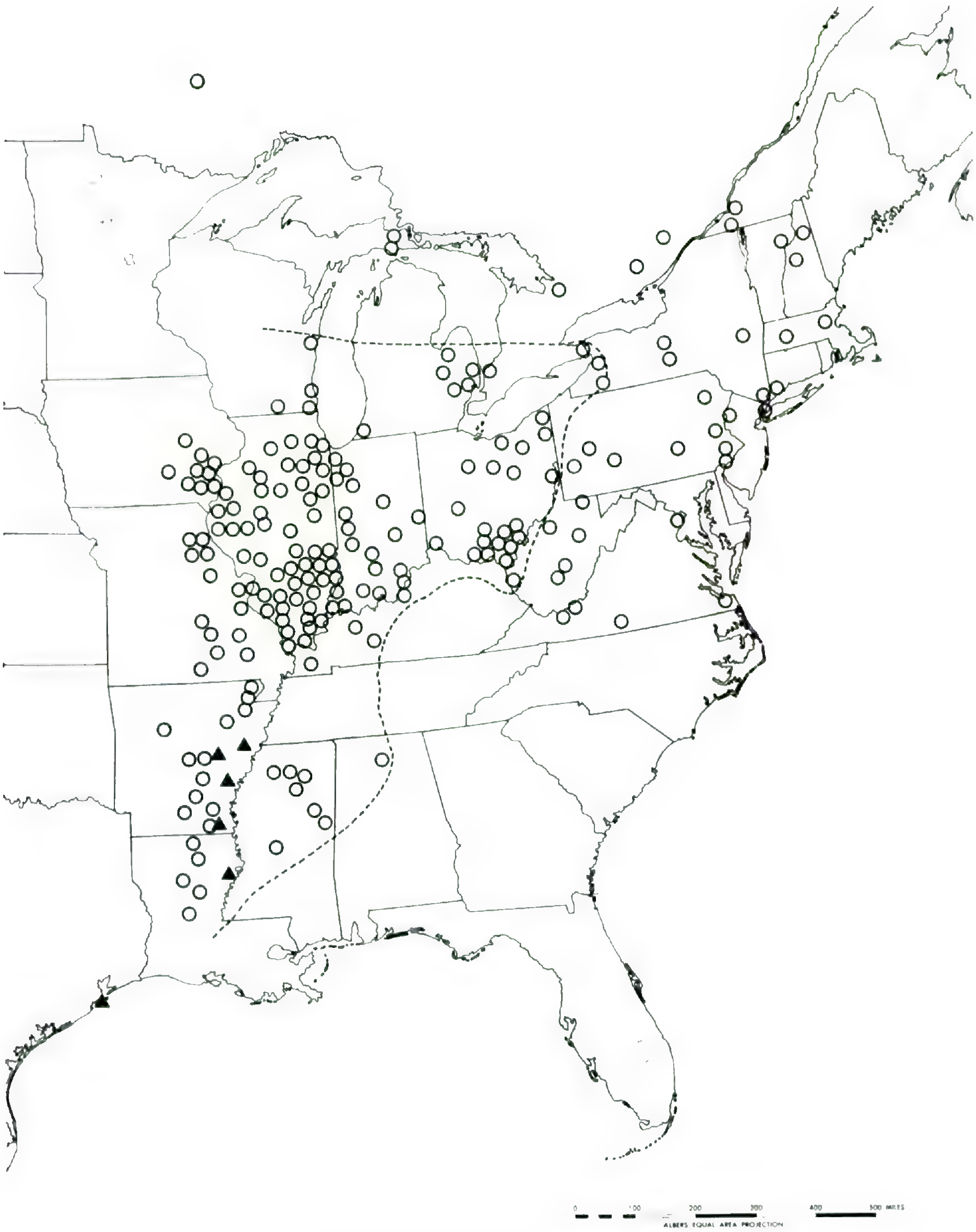


FIGURE 80. Distribution of *Oenothera pilosella* subsp. *pilosella* (circles) and subsp. *sessilis* (triangles). Dotted lines show the eastern and northern limits of the natural distribution.

populations. It may be assumed that any populations in the Atlantic Coast states and Canadian Maritime Provinces are local escapes from cultivation.

Illustration: Gleason (1963: 595).

This is again a variable taxon, although not nearly so much so as *O. fruticosa*. Among the notable morphological characters which show considerable variation are the following:

1. *Habit*: Usually strongly rhizomatous, forming large colonies. Stems of many populations are all simple, others all branched toward the upper portions of the plant, or both simple and branched stems may occur within a single population. The branches are usually at wide angles to the main axis, or in some populations more strongly ascending.

2. *Pubescence*: The taxon is characterized by long (ca. 2 mm) erect hairs on the stems, inflorescences, and sometimes the leaves. The pubescence varies from white to yellowish or tawny. There are frequently subglabrous individuals within typical pubescent populations as in Jackson Co., OH, 29 June 1932, *Bartley & Pontius* (OS) and Athens Co., OH, *Straley 980* (MO). The leaves are usually sparsely to densely strigose with shorter (1 mm) or longer (2 mm) hairs, but they may be subglabrous with ciliate margins. The mature capsules vary from densely strigose with hairs 2–3 mm long as in Monroe Co., MO, *Hudson 518* (MO) to very sparsely pubescent or glabrous as in Howell Co., MO, *Steyermark 78703* (F, GH, MO), the type of *O. pilosella* f. *laevigata* Palmer & Steyermark.

3. *Leaves* (Figs. 21–28): These are quite variable in size, shape, and pubescence. Cauline leaves are usually subsessile although they may be borne on petioles to 2 cm long. Leaf shape ranges from linear as in collections from Effingham Co., IL, *Evers 16959* (ILLS) and Little River Co., AR, *Tucker 16146* (MO), to elliptic or ovate as in Gallia Co., OH, *Straley 925* (MO) and Knox Co., MA, *Straley 787* (MO). Populations from the southern portion of the range tend to have narrower leaves than those from the north, but there are many exceptions and variations in leaf width within populations. Margins of leaves are subentire to remotely dentate. Leaves are usually held at nearly right angles to the primary axis, although they may be more or less ascending.

4. *Capsules*: These vary in size, stipe length, shape, and pubescence. Size ranges from very short capsules 5–7 mm long which are sessile or on a short stipe (1 mm) as in Pope Co., AR, *Tucker 15500* (MO), to long capsules 16–18 mm long on a stipe 10–12 mm long as in Adams Co., OH, July 1972, *Bartley 23* (OS). Capsule shape varies from linear-elliptic or elliptic to linear-clavate.

Among populations assigned to this taxon which approach *O. pilosella* subsp. *sessilis* in leaf shape and width and in capsule shape, but with long erect hairs on the stems, and with rhizomes are collections from La Salle Parish, LA, *McVaugh 8482* (NA); Rapides Parish, LA, *Kral 20065* (VDB); and Lonoke Co., AR, *Demaree 22938* (BH, CU, ISC, MO, NO, NY, OKLA, TENN).

There are no previous chromosome reports for this taxon except a probable octoploid ($n = 28$) (DeTurck, 1969). An octoploid chromosome number reported by Hecht (1942) from Cook Co., Illinois, as *O. fruticosa* doubtlessly refers to *O. pilosella* (A. Hecht, pers. comm.). *Oenothera fruticosa* does not occur near Chicago, whereas *O. pilosella* is (or was) frequent.

Vouchers for chromosome number (24 individuals, 14 populations): Octoploid, $n = 28$. ARKANSAS: Ashley Co., *Straley 1057*, 1 ring of 8, 5 rings of 6, 1 ring of 4, 7 pairs. Cleveland Co., *Straley 1069*. Drew Co., *Straley 1052*. OHIO: Athens Co., *Straley 923, 933, 980*. Gallia Co., *Straley 925, 926, 927*. Pike Co., *Straley 943*. CULTIVATED: KENTUCKY: Harlan Co., *Straley 694*. MAINE: Washington Co., *Straley 802*. OHIO: Athens Co., *Straley 924*. VIRGINIA: Giles Co., *Straley 709*.

2b. **Oenothera pilosella** subsp. **sessilis** (Pennell) Straley, comb. nov.

Kneiffia sessilis Pennell, Bull. Torrey Bot. Club 46: 366. 1919.
Oenothera sessilis (Pennell) Munz, Bull. Torrey Bot. Club 64: 291. 1937.

Perennial herb 3–6.5 dm tall, from a distinctly thickened, ± bulbous rootstock to 1 cm thick. Stems simple to few branched in the upper third, the branches ascending, densely strigose with hairs less than 1 mm long throughout, except near the base, where subglabrous. Basal leaves oblanceolate, subglabrous with ciliate, undulate margins, 2.5–7 cm long; 0.7–2.3 cm wide, the petiole 1–1.5 cm long; cauline leaves ± ascending, lanceolate to narrowly lanceolate (3–)6–7(–9) cm long, (0.3–)0.6–0.8(–1.1) cm wide, sessile, subentire. Ovary 4.5–6.5(–8) mm long, 1–1.5(–2) mm thick, oblong, sessile. Floral tube 10–15(–20) mm long. Sepals 10–18 mm long, 2–3 mm wide, the tips 1–2 mm long, connivent to ± divergent. Petals 1.5–2.5 cm long, 1.8–2.2 cm wide, obcordate, dark yellow. Filaments 7–9 mm long; anthers 5–8 mm long; pollen ca. 145 μm in diameter. Style 10–12 mm long; stigmatic lobes 2–4 mm long. Capsule elliptic, 8–10 mm long, 3–4 mm thick, 4-angled, not winged, sessile or with a stipe 1–2 mm long. Gametic chromosome number, $n = 28$. Self-incompatible.

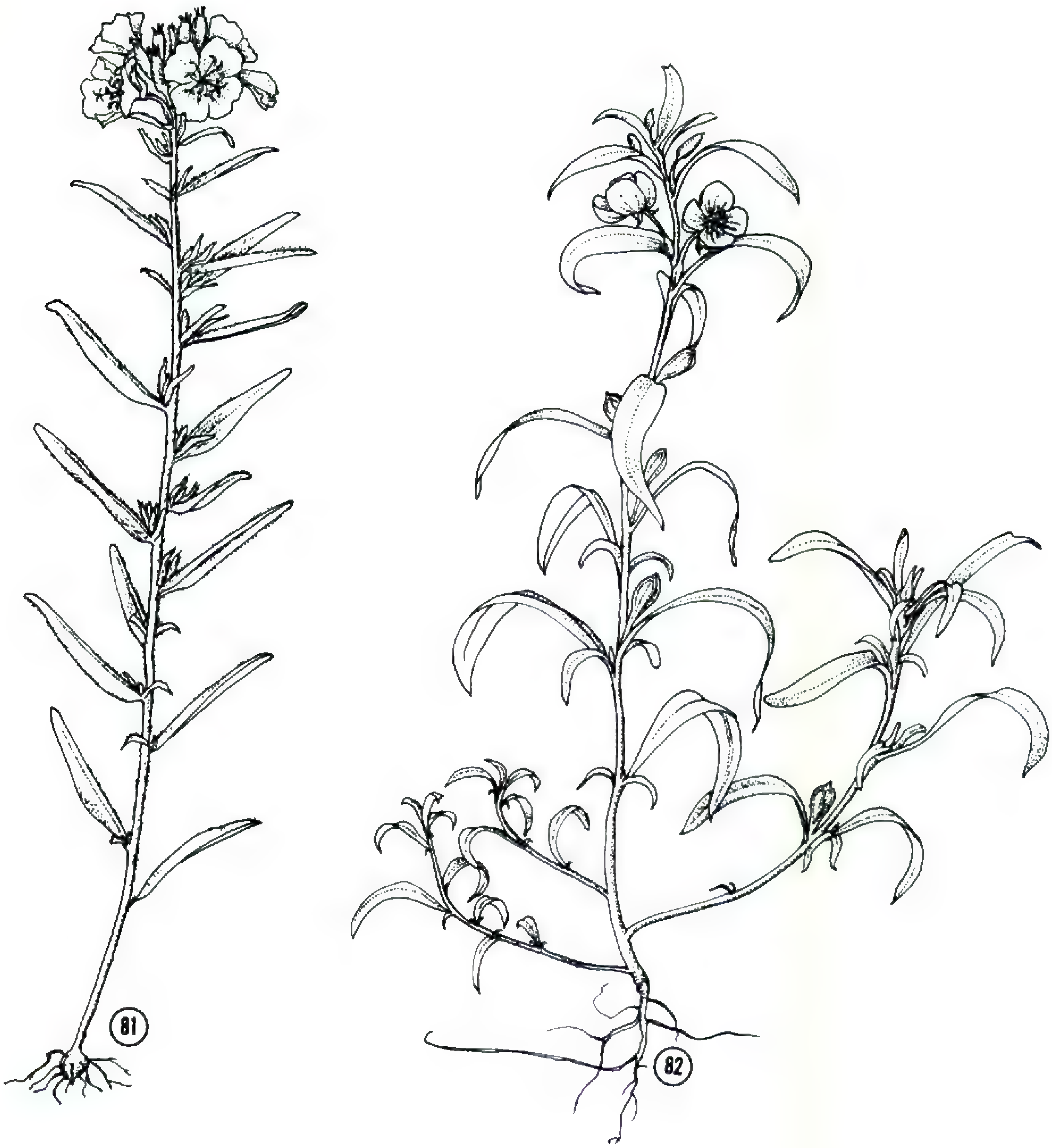
Type: Arkansas, Little Rock Co., Little Rock, 2 June 1885, *H. E. Hasse* (NY).

Distribution (Fig. 80): Presently limited to remnant wet or usually dry prairies of eastern Arkansas, central Louisiana, and the Gulf Coast of Texas, possibly surviving only in eastern Arkansas.

Illustration: Fig. 81.

Specimens examined: ARKANSAS: Arkansas Co.: DeWitt, riceland prairies, *Demaree 21078* (BH, MO, NY, SMU). Near Hagler, flat upland, *Chamberlain 33* (ILL). 3 mi SW of Stuttgart, prairie, *Straley 1071*. Ashley Co.: Mist, prairies, *Demaree 15086* (POM, SMU). Prairie Co.: *Wheeler 57* (F, MICH). Near Hazen, Grand Prairie, *Palmer 25038* (MO). St. Francis Co.: Forrest City, valley land, *Demaree 15107* (BH, SMU). LOUISIANA: Tensus Parish: *Hale s.n.* (MICH). TEXAS: Galveston Co.: Galveston Island, *Lindheimer s.n.* (US). WITHOUT LOCALITY: *Hale s.n.* (MASS, NY, P). WITHOUT DATA: (NY, US).

This taxon, named by Pennell (1919) and retained as a species by Munz (1937, 1965), is treated as a subspecies of *O. pilosella*, based on chromosome number and morphological similarities. It is rarely collected and differs from *O. pilosella* subsp. *pilosella* in the following characteristics. It is apparently not rhizomatous, although some populations may be so. In the only two extant populations which have been located, Arkansas Co., AR, *Straley 1071* (MO) and Prairie Co., AR, *Straley 1049* (MO), basal rosettes are produced directly from the rootstock of the current year or on a very short, ± woody extension of the spherical rootstock which cannot be called a rhizome. Both the branches and leaves are more ascending than in *O. pilosella* subsp. *pilosella* and the leaves are typically narrower. The pubescence is of short (1 mm or less), dense, appressed hairs throughout. The sepal tips are usually ± connivent in bud. The ovaries and mature capsules are usually elliptic with a short stipe. Collections from Ashley Co., AR, *Demaree 15086* (POM, SMU) assigned to this taxon are somewhat intermediate to subsp. *pilosella* in the long erect hairs on their stems, but have the general aspect of *O. pilosella* subsp. *sessilis*. Another collection which



FIGURES 81–82.—81. *Oenothera pilosella* subsp. *sessilis* (×⅓). [After *Straley 1049* (MO).]—82. *O. spachiana* (×½). [After *Emig 582* (MO).]

seems best assigned to subsp. *sessilis* is from Little Rock, AR, 26 May 1885 *Hasse* (NY) and is densely, short strigose throughout, lacking any long hairs. However, it has broader leaves, more typical of subsp. *pilosella*. A specimen with leaves of similar size and shape from near Corning, Clay Co., AR, 25 May 1893, *Eggert* (MO), has the strigose vestiture of subsp. *sessilis*—although distinctly yellowish—more typical of subsp. *pilosella*. These collections lack good underground parts and mature fruits, with which they could be more definitely assigned to one subspecies or the other.

Pennell's type specimen of this taxon was presumably collected by Hasse in the vicinity of Little Rock, although the hilly uplands around the city of present-day Little Rock are somewhat out of line with the ecology of the presently known

populations of this subspecies. However, Hasse's collection may have been from the flatter, lowlands east or south of the city, or even many miles from the city. Munz was apparently confused between this entity and some populations of *O. fruticosa* from the same general area. Munz (1937: 291) states that *O. sessilis* is distinct "from *O. fruticosa* in the narrower, more elongate capsules," when, in fact, all of the mature capsules of this taxon are neither as narrow nor as elongated as capsules of *O. fruticosa*. However, most of the specimens of subsp. *sessilis* which Munz probably saw have immature capsules. At any rate, the type collection, other specimens cited above, and the two known extant populations certainly represent a distinctive, yet apparently rare taxon.

Vouchers for chromosome number (3 individuals, 2 populations): Octoploid, $n = 28$. ARKANSAS: Arkansas Co., *Straley 1071*. Prairie Co., *Straley 1049*.

3. **Oenothera perennis** L., Syst. Nat., ed. 10. 998. 1758.

O. pumila L., Sp. Pl., ed. 2. 493. 1762, illeg. subst. Based on *O. perennis* L.
O. pusilla Michx., Fl. Bor. Amer. 1: 225. 1803. TYPE: Canada, Québec, Lake Mistassini, in stony places, *A. Michaux* (P); Munz, Bull. Torrey Bot. Club 64: 303. 1937.
O. chrysantha Michx., Fl. Bor. Amer. 1: 225. 1803. TYPE: Canada, Québec, *A. Michaux* (P); Munz, Bull. Torrey Bot. Club 64: 303. 1937.
O. pumila L. var. *minima* Lehm. in Hook., Fl. Bor. Amer. 1: 212. 1833. Based on *O. pusilla* Michx.
Kneiffia pumila (L.) Spach, Hist Nat. Vég. Phan. 4: 377. 1835.
K. chrysantha (Michx.) Spach, Nouv. Ann. Mus. Hist. Nat. 4: 368. 1835.
K. michauxii Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 167. 1835, illeg. subst. Based on *Oenothera pumila* L. and *O. gracilis*.
Oenothera pumila L. var. *pusilla* (Michx.) Walp., Repert. Bot. Syst. 2: 84. 1843.
O. pumila L. var. *chrysantha* Gordinier & Howe, Fl. Renssalaer Co., N.Y. 14. 1894. TYPE: New York, Renssalaer Co., Postenkill, *E. C. Howe* (not located).
O. pumila L. var. *rectipilis* S. F. Blake, Rhodora 19: 110. 1917. TYPE: Canada, New Brunswick, Petit Rocher, 21 Aug. 1913, *Blake 5513* (GH, holotype; CU, NY, P, TEX, US, isotypes).
Kneiffia perennis (L.) Pennell, Bull. Torrey Bot. Club 46: 372. 1919.
K. depauperata O. Jennings, J. Wash. Acad. Sci. 10: 454. 1920. TYPE: Canada, Ontario, northeast of Sioux Lookout, shore of a boulder-strewn bay of the lake, 7 Sep. 1914, *O. E. & G. K. Jennings 7501* (CM).
Oenothera perennis L. var. *rectipilis* (S. F. Blake) S. F. Blake, Rhodora 25: 47. 1923.

Perennial herb from fibrous rootstock. Stems simple or clumped and branching above, usually erect to slightly decumbent, (0.3–)1.5–3(–7.5) dm tall, with short (ca. 0.5 mm long) straight or incurved hairs, the upper parts, especially the inflorescences, glandular puberulent. Overwintering basal rosette withered by early anthesis. Basal leaves oblanceolate to obovate, 2–4 cm long, 0.2–1.2 cm wide, glabrous except for the ciliate margins, the petiole (0.2–)0.5–1.2(–2.5) cm long; cauline leaves oblanceolate to obovate, 3–7 cm long, 0.2–1.2 cm wide, narrowing to a winged petiole 0.1–1 cm long, sparsely strigose, the margins ciliate. Inflorescence nodding, glandular pubescent, relatively few flowered; subtending leafy bracts 8–18 mm long, 1–2 mm wide. Ovary 6–12 mm long, 1–2 mm thick. Floral tube 3–10 mm long. Sepals 2–4 mm long, 0.5–1 mm wide, the tips less than 1 mm long, connivent. Petals 5–10 mm long, 4–10 mm wide, truncate to cleft, dark yellow. Filaments 3–4 mm long, erect; anthers 1–2 mm long, shedding pollen directly on the stigma at anthesis; pollen ca. 108 μm across, 32–54% empty. Style 3–4 mm long, erect; stigmatic lobes about 1 mm long, di-

vergent. Capsule tetragonal or narrowly winged, clavate, glandular-puberulent, 5–10 mm long, 2–3 mm thick, tapering to a short stipe 1–2 mm long. Seeds bright rusty brown, 0.7–0.8 mm long, 0.2–0.3 mm thick, papillose. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I). Autogamous, often in bud; complex heterozygote.

Lectotype: Miller, Figs. Pl. 2: *188*. 1757. Drawn from a plant grown at Chelsea Physic Garden from seeds received from the Trianon, originally of Canadian origin.

Distribution (Fig. 83): Fields, open woods, and boggy areas from Newfoundland to southeastern Manitoba, south along the mountains to South Carolina, less common westward to Missouri. Isolated collections have been seen from coastal North Carolina, Hertford Co., (NCU) and British Columbia, New Westminster (CAN, UBC) and Shawnigan Lake, Victoria Island (Melburn, 1965), where it is probably persistent as a garden escape. One collection, *Macoun 482* (US) from "Saskatchewan Plains" is doubtfully from the province of Saskatchewan, but may be from Saskatchewan Co., Manitoba.

Illustration: Gleason (1963: 595).

This is the most distinct and least variable taxon among the perennial species of sect. *Kneiffia,* but it does vary in the following characters:

1. *Habit*: Occasionally very short plants flower and fruit. An especially small collection only 3 cm tall is from Lake St. John Co., Québec, 24 July 1892, *Kennedy* (GH). Very tall plants (6.5–7.5 dm tall) are included in collections from Franklin Co., ME, *Seymour & Potter 24333* (VT) and York Co., ME, *Straley 1096* (MO). Stems are usually simple or few branched. A collection from Washington Co., ME, *Fernald 1998* (NEBC) has 32 branches from the base. Others from Digby Co., Nova Scotia, *Graves 22002* (PH) and Cheshire Co., NH, *Massey & Boufford 4139* (NCU) are much branched higher on the plant.

2. *Pubescence*: Most plants have the lower two-thirds of the stem clothed with short (0.5 mm) appressed or incurved hairs. Some collections, particularly from eastern Canada, have stiff erect hairs (0.5 mm) on the stems and have been known in the past as var. *rectipilis* S. F. Blake. But single collections often include some plants with erect hairs and others with appressed hairs: Carleton Co., New Brunswick, 30 May 1952, *Slipp* (DAO) and King's Co., New Brunswick, *Straley 1098* (MO). Other collections—e.g., Montmorency Co., Québec, 28 June 1905, *Macoun* (GH, NY) and Missisquoi Co., Québec, *Raymond & Champagne 1401* (DAO)—include plants with either erect straight hairs, appressed hairs, mixtures of these, or nearly glabrous stems. Occasional collections have densely strigose leaves clothed with white hairs to 0.5 mm long, among which are collections from Muskegon Co., MI, *Bazuin 6597* (MICH) and Thunder Bay District, Ontario, *Garton 10468* (CAN).

3. *Leaves* (Figs. 33–39): These differ in size, but there is little difference in shape compared with that in other perennial taxa of the section. Plants from the southern Appalachians often have narrower leaves. There are occasional collections with very narrow leaves (1.5–2 mm wide) as: Tompkins Co., NY, 15

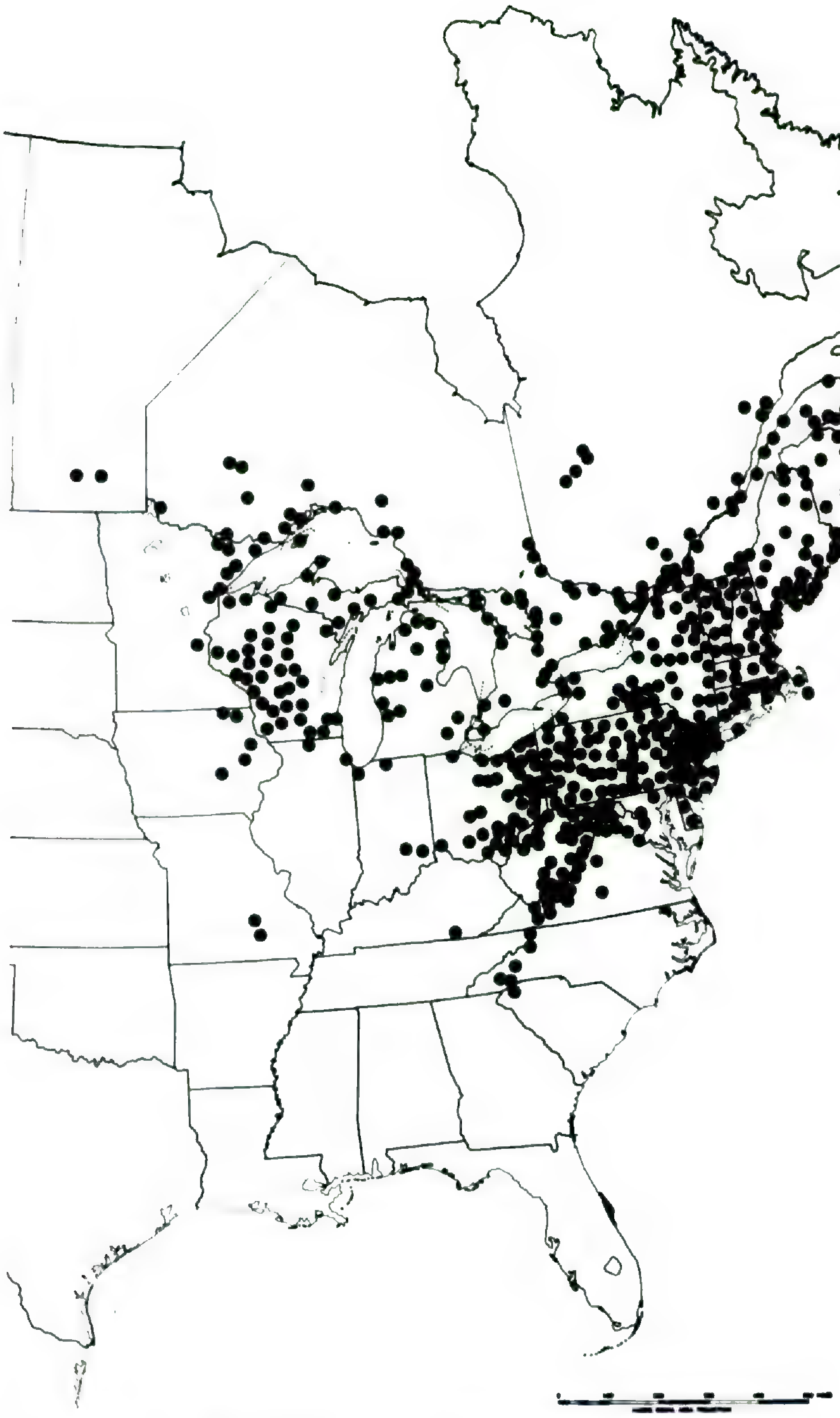


FIGURE 83. Distribution of *Oenothera perennis*.

June 1903, *Jackson* (WIS). An unusual collection from a bog in Muskegon Co., MI, *Voss 9164* (MICH), is much branched, with widely spaced bractlike leaves (0.5–2 mm wide and 10 mm long) throughout most of the plant.

4. *Inflorescences and flowers*: The inflorescences are characteristically nodding in bud, gradually becoming erect as the flowers open. Frequently, depauperate plants with only a few flowers do not have nodding tips. Plants with unusually small flowers (petals 3–4 mm long) include: Hillsborough Co., NH, 12 July 1916, *Batchelder* (NEBC) and Guernsey Co., OH, *Laughlin 1151* (OS). Larger-flowered collections (petals 10 mm or more long) include, among

others: Coos Co., NH, *Pease 16403* (NEBC) and Hancock Co., ME, 14 June 1889, *Rand & Renfield* (NEBC). Plants from the southern part of the range often have smaller flowers. Cleistogamous flowers have not been observed in nature, but are suspected in collections from Grafton Co., NH, *Fernald 11817* (NEBC) and Pontiac Co., Québec, *Dore 20883* (TRT) in which part of the large, unopened flower buds are dropping from the ovaries, which otherwise appear normal. Examination of the buds in these collections shows that pollen had been shed in the stigmatic lobes, as usual in the species.

Valcanover (1927) reports a chromosome number of $n = 14$ for this taxon, with no reference to the origin of the population. In light of recent chromosome number determinations it is suspected that Valcanover's count actually refers to *O. fruticosa*. An herbarium voucher from Ottawa, Ontario, 12 July 1964, *Mosquin* (DAO) was annotated as having a ring of 14 chromosomes by Raven. A report by Kapoor (1972) of $2n = 49$ made from a root-tip preparation of a population from Halifax Co., Nova Scotia, seems most doubtful. It seems virtually certain that Kapoor's $2n = 49$ number refers to some other plant species and that his root-tip fixations or preparations were mixed. Kapoor (pers. comm.) also made a determination of $n = 7$ in plants of *O. perennis* from the same area but did not report it. This population was sampled in 1975 and only diploid plants with a ring of 14 chromosomes were found.

Vouchers for chromosome number (59 individuals, 19 populations): $n = 7$. CANADA: NEW BRUNSWICK: Carleton Co., *Straley 1113*, ring of 14. Kings Co., *Straley 803, 1098*, ring of 14. York Co., *Straley 1111*, ring of 14. NOVA SCOTIA: Halifax Co., *Straley 1100*, ring of 14; *1101*, ring of 14; *Straley 1102*, ring of 14. PRINCE EDWARD ISLAND: Kings Co., *Straley 1105*. Queens Co., *Straley 1107*. UNITED STATES: MAINE: Knox Co., *Straley 824*, ring of 14. Waldo Co., *Straley 793, 1097*. York Co., *Straley 1096*, ring of 14. NEW HAMPSHIRE: Grafton Co., *Straley 774*. NEW YORK: Columbia Co., *Straley 1095*. VIRGINIA: Craig Co., *Straley 719*, ring of 14. Montgomery Co., *Straley 753*, ring of 14. WEST VIRGINIA: Nicolas Co., *Straley 692*. CULTIVATED: NORWAY: Seeds from Botanical Garden, University of Bergen, *Straley 693*, ring of 14.

4. **Oenothera spachiana** Torr. & A. Gray, Fl. N. Amer. 1: 498. 1840.

Blennoderma drummondii Spach, Nouv. Ann. Mus. Hist. Nat. 4: 407. 1835. LECTOTYPE: Texas, 1834, *T. Drummond 81* (P; G, GH, K, isolectotypes).
Oenothera drummondii (Spach) Walp., Repert. Bot. Syst. 2: 85. 1843, non Hook., 1835.
O. uncinata Scheele, Linnaea 21: 578. 1848. TYPE: Texas, Harris Co., prairie near Houston, *Romer* (not located).
Kneiffia spachiana (Torr. & A. Gray) Small, Bull. Torrey Bot. Club 23: 179. 1896.
Onothera fruticosa L. race *spachiana* (Torr. & A. Gray) H. Lév., Monogr. Onoth. 106. 1902.

Slender, erect annual herb 1–3(–4.5) dm tall from a sparsely branched taproot. Stems usually simple or with a few ascending branches from the base or higher, densely strigose throughout. Basal leaves 2–5 cm long, 0.5–1.5 cm wide, oblanceolate to elliptic, subentire, narrowing to a distinctly winged petiole 0.5–2.0 cm long, usually persistent to early flowering; cauline leaves narrowly oblong-lanceolate to oblong-linear, 3–6 cm long, 0.2–0.6 cm wide, the petiole 0.2–0.6(–1.5) cm long. Flowers in leaf axils of upper ½ or ⅔ of plant. Ovary 8–12 mm long, 1–2 mm thick. Floral tube 4–10 mm long. Sepals 4–8 mm long, 1–2 mm wide, the free tips to 1 mm long. Petals 5–14 mm long, 10–15 mm wide, truncate to emarginate, pale yellow, turning pink, especially along the veins,

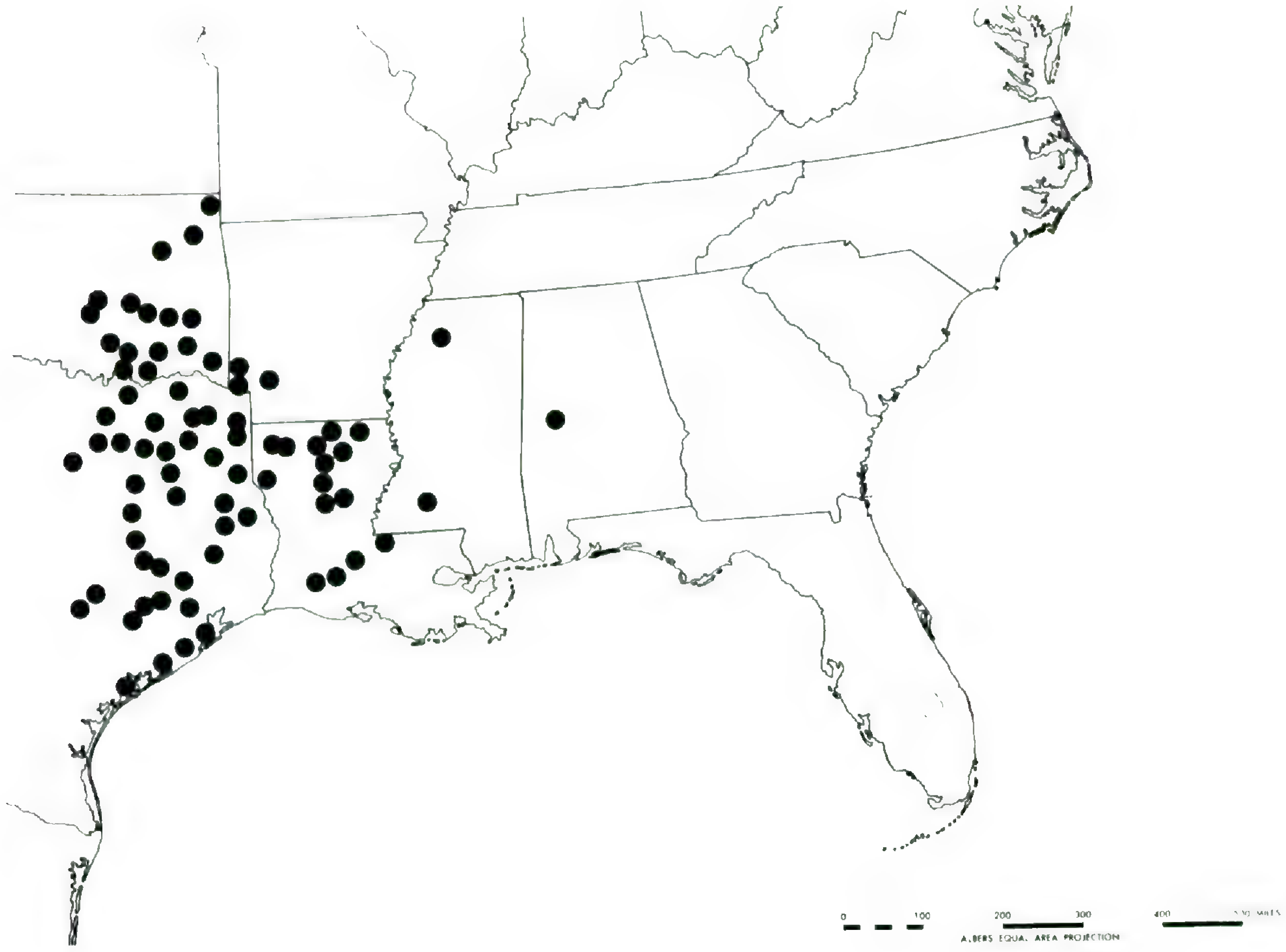


FIGURE 84. Distribution of *Oenothera spachiana.*

after pollination. Filaments 3–7 mm long; anthers 2–4 mm long, shedding pollen directly on the stigma in bud; pollen ca. 70 μm in diameter. Style 3–7 mm long; stigmatic lobes linear, connivent, 1–2 mm long. Fruit broadly clavate, 4-angled, 5–15 mm long, 3–5 mm wide, sessile, with a narrowed sterile base. Seeds straw colored, 1 mm long, 0.5 mm wide, verrucose. Gametic chromosome number, $n = 7$. Autogamous, usually in bud, often cleistogamous.

Type: Texas, *T. Drummond 81* (P, holotype; GH, isotype).

Distribution (Fig. 84): Prairies, open roadsides and sandy places from eastern Oklahoma and eastern Texas to southeastern Arkansas and Louisiana. Populations in Panola and Lincoln counties, Mississippi and Hale Co., Alabama are apparently native, though possibly introduced. This species has also been collected as a ballast weed in Camden Co., New Jersey (NA). Scattered, but forming large populations.

Illustration: Fig. 82.

A relatively uniform taxon, morphologically, in pubescence, leaf and capsule size and shape, but variable in the following characters:

1. *Habit*: Usually simple stems but may be much branched from the base (8–15 branches) as in collections from West Feliciana Parish, LA, *Cooley & Brass 414* (GH, NCU) and Van Zandt Co., TX, *Cory 57378* (SMU). Unusually small plants (7–9 cm tall) in flower are from Brazoria Co., TX, *Palmer 5047* (POM).

2. *Flowers*: Collections with small flowers (petals 5–6 mm long) include those from Marshall Co., OK, *Goodman 5823* (GH, OKL) and St. Augustine Co., TX, *Palmer 9486* (US). Large-flowered collections (petals to 15 mm long) include those from Little River Co., AR, *Moore 510120* (WISC) and Grant Parish, LA, *Shinners 31703* (OKL, SMU). Cleistogamous flowers are frequent in this taxon, with some populations apparently having all flowers cleistogamous. Some plants form both normal and cleistogamous flowers, and the proportion is probably under environmental control. Notable collections with cleistogamous flowers include those from Hampstead Co., AR, *Bush 1428* (GH, MO, RSA) and Marshall Co., OK, *Waterfall 11448* (OKLA). Plants raised from seed from Union Parish, LA, *Straley 751* produced only normal flowers early in the season and only clesitogamous flowers later. The following year progeny from this collection produced plants with only cleistogamous flowers.

Gregory & Klein (1960) report this taxon as diploid with 7 bivalents during meiosis from collections raised from seed from Marshall Co., OK, *Waterfall 11448* (OKLA, RSA).

Voucher for chromosome number (3 individuals, 1 population): Diploid, $n = 7$. LOUISIANA: Union Parish, *Straley 751*.

Subsection II. PENIOPHYLLUM

Oenothera sect. **Kneiffia** subsect. **Peniophyllum** (Pennell) Straley, comb. nov. Based on *Peniophyllum* Pennell, Bull. Torrey Bot. Club 46: 373. 1919.

Oenothera subgen. *Kneiffia* (Spach) Munz sect. *Peniophyllum* (Pennell) Munz, Bull. Torrey Bot. Club 64: 288. 1937; N. Amer. Fl., ser. 2, 5: 85. 1965.

Erect annual herbs. Stems simple or with many ascending branches, villous near the base. Basal leaves ovate to obovate; cauline leaves linear. Inflorescences erect, strigulose to glandular puberulent; floral bracts shorter than the subtending ovaries. Sepals without free tips. Petals pale yellow, flushed with pink after fertilization. Stigma surrounded by anthers at anthesis, the lobes blunt. Flowers sometimes cleistogamous. Capsules sessile, ellipsoid, rhomboid, 4-ridged. Gametic chromosome number, $n = 7$. Autogamous or cleistogamous.

Type species: *Oenothera linifolia* Nutt.

5. **Oenothera linifolia** Nutt., J. Acad. Nat. Sci. Philadelphia 2: 120. 1821.

Kneiffia linifolia (Nutt.) Spach, Nouv. Ann. Mus. Hist. Nat. 4: 368. 1835.
K. linearifolia Spach, Ann. Sci. Nat. Bot., sér 2, 4: 167. 1835, illeg. subst. Based on *Oenothera linifolia* Nutt.
Peniophyllum linifolium (Nutt.) Pennell, Bull. Torrey Bot. Club 46: 373. 1919.
Oenothera linifolia Nutt. var. *glandulosa* Munz, Bull. Torrey Bot. Club 64: 289. 1937. TYPE: Georgia, DeKalb Co., Little Stone Mountain, thin soil overlying rocks, 11 May 1901, *A. Curtiss 6778* (GH, holotype; G, GA, GH, ILL, K, NA, NY, OKL, P, US, isotypes).

Erect annual herb 1–5 dm tall from a sparsely branched taproot. Stems simple or with a few to many ascending branches from near the base or higher. Short erect hairs (0.2–0.4 mm long) near the base, occasional hairs on the margins of the leaves, the plants strigillose to glandular puberulent above, especially in the inflorescences. Basal leaves ovate to obovate or narrowly elliptic, 1–2(–4) cm

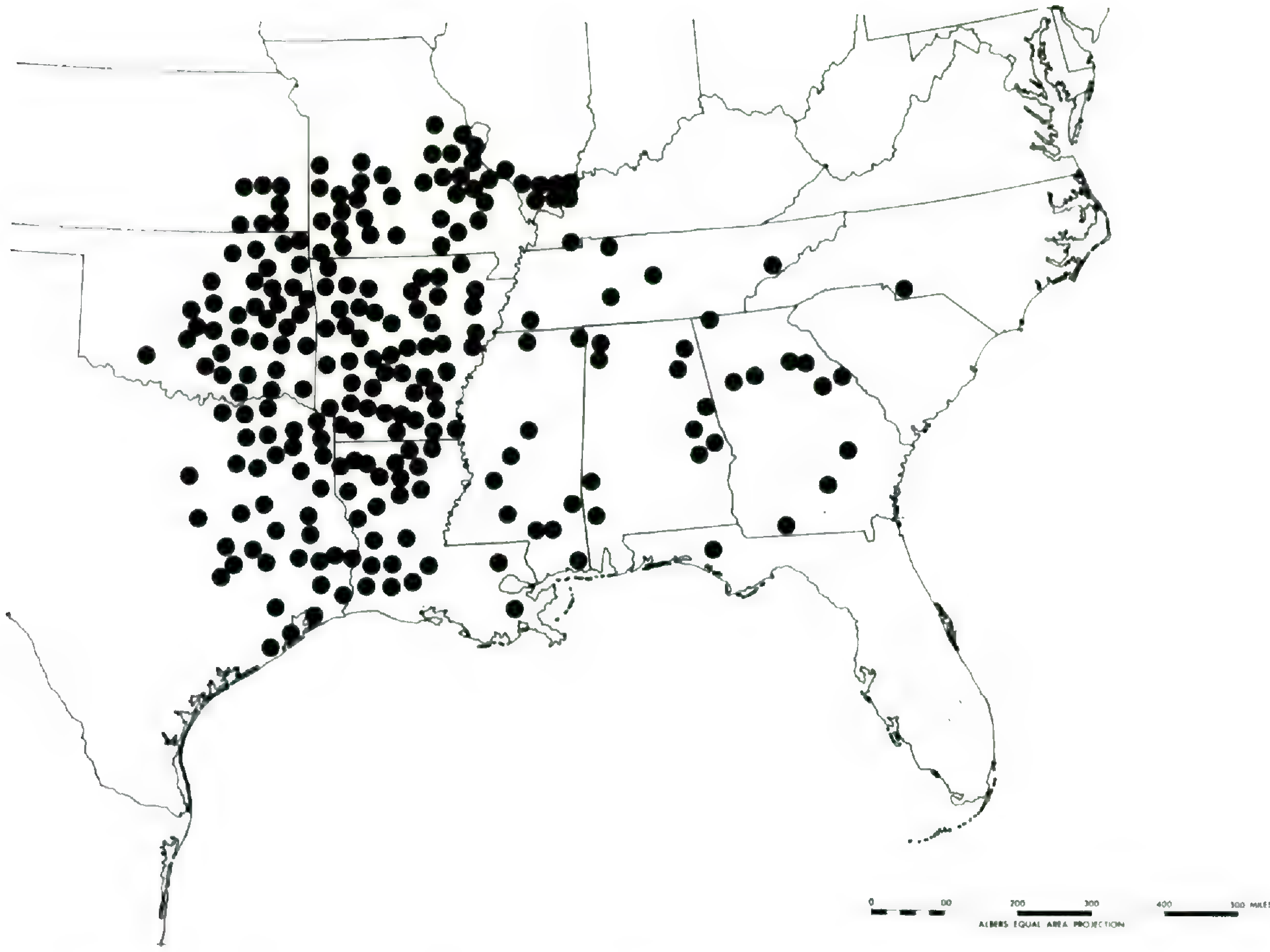


Figure 85. Distribution of *Oenothera linifolia*.

long, 0.2–0.6 cm wide, narrowing to a winged petiole 0.2–1(–1.5) cm long, subentire to remotely dentate, glabrous to sparsely strigillose or glandular puberulent, especially along the petiole, usually not persistent to flowering time; lower cauline leaves becoming abruptly sessile and linear or filiform, less than 1 mm wide, 1–4 cm long, crowded. Inflorescences terminal, distinct, unbranched spikes (1–)3–6(–12) cm long, glandular puberulent to strigillose, the hairs 0.1–0.2 mm long; bracts ovate to deltoid-ovate, 0.5–2 mm long, 1–3 mm wide. Ovary 3–6 mm long, 0.5–1.5 mm thick. Floral tube 1–2 mm long. Sepals 1.5–2 mm long, 0.3–0.6 mm wide, without free tips. Petals 3–5(–7) mm long, 1–3(–4) mm wide, obcordate to cleft, bright yellow. Filaments 1–2 mm long; anthers 0.5–1.0 mm long, shedding pollen directly on the stigma before and during anthesis; pollen ca. 93 μm in diameter. Style 1–2 mm long; stigma 0.5 mm long, shallowly 4-lobed. Capsules sessile (or with short stipe 1–4 mm long), 4–6(–10) mm long, 1.5–3 mm thick, ellipsoid-rhomboid, 4-ridged. Seeds pale reddish brown, ca. 1 mm long, ca. 0.5 mm wide, minutely verrucose. Gametic chromosome number, $n = 7$. Autogamous, usually in bud; frequently cleistogamous.

Type: Arkansas, summits of arid hills and the shelvings of rocks, near the banks of the Arkansas River, *T. Nuttall* (PH-910101, holotype; BM, GH, K, NY, PH, US, isotypes).

Distribution (Fig. 85): Prairies, open rocky and sandy places, and open

roadsides, southern North Carolina to northern Florida, westward to southern Illinois, eastern Kansas and central Texas.

Illustration: Gleason (1963: 595).

This is the most distinctive and morphologically uniform taxon in the section. Variability in size and branching appears to be due largely to soil fertility and moisture levels during the growing season. Among the notable variations are the following:

1. *Habit*: Although the plants are usually simple, they may be much branched from the base as in collections from Poinsett Co., AR, *Demaree 29072* (SIU) and Johnston Co., OK, *Correll & Correll 25018* (TEX), with 12–20 branches. Other collections exhibit much branching higher on the plant (30–50) branches, or ascending secondary branches as in a collection from Washington Co., AR, *Wells 22* (US), with a thickened basal stem 5–6 mm in diameter near ground level, and in one from Independence Co., AR, *Demaree 26936* (RSA). Branching appears frequently to be the result of mechanical injury to the apex of the plant. The basal seedling rosette of leaves sometimes remains green during early flowering, probably in response to adequate moisture levels in the soil, as in collections from Stone Co., AR, *Demaree 64562* (SMU) and Latimer Co., OK, *Hopkins 1685* (POM).

2. *Pubescence*: Some collections with predominately glandular hairs on the inflorescences have been known as *O. linifolia* var. *glandulosa* Munz. There are, however, many individuals and populations intermediate to the more frequent form with predominately nonglandular, incurved hairs in the inflorescence. The continued taxonomic recognition of this variety appears to be without merit.

3. *Flowers*: Occasional individual plants or populations have very large flowers (petals 6.5–7 mm long) as in collections from Tangipahoa Parish, LA, 20 Apr. 1963, *Wilson* (FSU) and Drew Co., AR, *Demaree 14578* (NY).

4. *Capsules*: The shape varies from subglobose and scarcely angled, with the body of the capsule ca. 4 mm long and the stripe ca. 1 mm long, as in collections from Panola Co., TX, *Shinners 20151* and Randolph Co., AL, *McVaugh 8609* (MICH, TEX, US), to very elongated with the body ca. 6 mm long and the stipe 3–4 mm long as in collections from Izard Co., AR, *Demaree 31792* (GH) and Payne Co., OK, 26 May 1916, *Learn* (OKLA).

One previous report of chromosome number of $n = 7$, with 7 pairs, was made by Gregory & Klein (1960) from Montgomery Co., AR, *Munz & Gregory 23503* (RSA).

Vouchers for chromosome number (8 individuals, 4 populations): Diploid, $n = 7$. ARKANSAS: Conway Co., *Straley 967*, 7 pairs, *969*, 7 pairs, *974*. Prairie Co., *Straley 961*.

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THE SOUTH AMERICAN SPECIES OF *OENOTHERA* SECT. *OENOTHERA* (*RAIMANNIA*, *RENNERIA*; ONAGRACEAE)[1,2]

WERNER DIETRICH[3]

ABSTRACT

This paper provides an account of the native and naturalized South American species of *Oenothera* sect. *Oenothera* (Onagraceae). Included are 63 taxa (species and subspecies) of three subsections, of which 58 are native in South America and the remainder introduced from North America (*Oenothera laciniata* subsp. *laciniata*, *O. drummondii*, *O. villosa*) or possibly from Europe (*O. erythrosepala*, *O. biennis*). Subsection *Munzia* includes 57 taxa, subsect. *Raimannia* 3 (*O. laciniata* subsp. *laciniata*, *O. laciniata* subsp. *pubescens*, *O. drummondii*), and subsect. *Euoenothera* also 3 (*O. erythrosepala*, *O. villosa*, *O. biennis*).

The main focus of this monograph is a revision of the exclusively South American subsect. *Munzia*, which is divided into the three series *Renneria*, *Allochroa*, and *Clelandia*. All taxa were cultivated at the Botanical Institute of the University of Düsseldorf from one to

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[1] Dedicated to my wife and my children Nikola, Lorenz, Bernadette, Gabriel and Christoph.

[2] I would like to thank those who have made the completion of this study possible. Prof. Wilfried Stubbe not only allowed me to work on this problem but also most generously provided facilities in the Botanisches Institut at the University of Düsseldorf. Prof. Peter H. Raven made it possible for me to study for six months at the Missouri Botanical Garden, during which time I was also able to visit South America for two months. My work in St. Louis and in South America was supported by a grant from the U.S. National Science Foundation to Dr. Raven, who also translated this manuscript from German. His interest and cooperation were invaluable for my work, and useful discussions concerning it were also held with Prof. Stubbe, Dr. A. Basler, Dr. M. Drillisch, and Dr. H. Kutzelnigg.

Thanks are due to Prof. K. A. and Dr. K. Santarius, who undertook a five-month trip to South America in 1968 for the purpose of collecting seed samples of *Oenothera* and thereby added more than 2,000 strains to the collection at the University of Düsseldorf. Their trip, supported by the Deutsche Forschungsgemeinschaft, provided the materials that made the present study possible. Mr. J. D. Conrad accompanied me to South America in January and February, 1974, and helped greatly to make our trip a success. Many South American botanists contributed in one way or another to the success of our trip, but I would like to thank especially Dr. E. Bordaz (Asunción, Paraguay), the late Prof. Dr. A. Burkart (San Isidro, Argentina), F. Encarnación (Lima, Peru), Prof. Dr. A. T. Hunziker (Córdoba, Argentina), R. M. Klein (Itajai, Brazil), L. F. Lautenschlager (Asunción, Paraguay), and Prof. Dr. E. Vanzolini (São Paulo, Brazil).

My technical assistant, Mrs. L. Mencke, tirelessly and expertly performed the necessary services in the laboratory and garden that helped to make this study possible. I would also like to thank the gardeners of the University of Düsseldorf for their cultivation of *Oenothera* over a period of many years, and many students at the University who performed a variety of technical functions on these plants. Many botanists kindly contributed seeds for the study, and I am grateful to them. The University of Düsselfdorf and the Minister für Wissenschaft und Forschung des Landes Nordrheinwestfalen awarded me a "Forschungsfreisemester" for the purpose of this study, and I am most grateful to them.

Finally, I would like to thank my wife and four children for their patience and understanding. I hope that the successful conclusion of my work represented by this revision will help to make up in part for the six months that we were apart during the course of its completion.

Material from the following herbaria was examined, and I am grateful to those who made the material in their charge available for study: AAU, AI (by Raven), AK, AMD, B, BA, BAA, BAB, BAS, BB, BM, BR, BREM, C, COI, CONC, CORD, CTES, DUSS, E, F, FR, G, GH, GOET, HB, HBG, HBR, K, L, LD, LE, LIL, LISE, LISU, LP, LY, M, MEL, MICH, MO, MPU, MVFA, ND, NSW, NY, P, PERTH, POM, PR, PRC, PRE, R, RAW (by Raven), RB, RSA, S, SGO, SI, SP, SRGH, UC, UPS, US, USM, W, Z, and the private Herbarium of Dr. A. Ruiz Leal, Godoy Cruz, Mendoza, Argentina (Leal).

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several wild strains. Cytological examination of meiosis in 600 plants representing 280 strains showed that 20 taxa were chromosomally homozygous, forming 7 bivalents at meiotic metaphase I. All other taxa were complex heterozygotes forming a ring of 14 chromosomes at meiotic metaphase I or with a smaller but still stable ring configuration (ring of 12 and 1 bivalent, ring of 8 and ring of 6, or ring of 10 and ring of 4). Homozygous species were distributed throughout the range of subsect. *Munzia*. Some of the individual chromosomally homozygous species also had individual wide ranges; for example, *O. scabra* and *O. versicolor* (series *Renneria*), *O. mendocinensis*, *O. odorata*, *O. indecora*, *O. affinis*, and *O. ravenii* (series *Allochroa*).

The following species of subsect. *Munzia* were adventive or established outside of South America: (1) *O. mendocinensis*: Europe (adventive); (2) *O. longiflora* subsp. *longiflora*: Europe, Atlantic Islands (Azores, Madeira, Canary Islands, Cape Verde Islands), South Africa, Australia; (3) *O. indecora* subsp. *indecora*: Europe (adventive); (4) *O. indecora* subsp. *bonariensis*: Europe (adventive), Australia, South Africa, Tristan da Cunha (adventive?); (5) *O. affinis*: Europe, India, Pakistan, Australia, Hawaii, South Africa; (6) *O. mollissima*: U.S.A. (adventive?), Australia; (7) *O. stricta* subsp. *stricta*: U.S.A., Mexico, Hawaii, Europe, Japan, India, Pakistan, Sri Lanka, Java, Australia, New Zealand, North Africa, South Africa, Ethiopia; (8) *O. parodiana* subsp. *parodiana*: South Africa, Europe (adventive).

The common ancestor of *Oenothera* sect. *Oenothera* subsect. *Munzia* seems to have arrived in South America from North America no more than a few million years ago, and to have given rise to some 57 taxa there subsequently in response to drastic climatic changes and increasing elevation of the mountains in that continent. *Oenothera laciniata* subsp. *pubescens* seems to have arrived in South America from North America much more recently, perhaps within the past 100,000 years.

Oenothera has been the subject of genetic and evolutionary investigations for a very long time, owing mainly to its unusual genetic system, which involves complex heterozygosity. The species of the so-called "*Euoenothera*" group of North America have been intensively studied for more than 70 years (summary, Cleland, 1972), but other members of the genus have not been considered in such depth. In Düsseldorf, a program has been conducted for more than 15 years on the biosystematics of the South American species of *Renneria* (Fischer, 1962) and *Raimannia* (Munz, 1935). In this work an extraordinarily rich array of wild populations of the group assembled under the direction of Professor Doctor Wilfried Stubbe has been utilized. The object has in part been to work out a more satisfactory taxonomic rearrangement of the South American species of these two closely related groups. Extensive investigations of the genetics of both groups had been carried out earlier by Professor J. Schwemmle of Erlangen and his students, but the results have not, for the most part, been applied to the systematics of these taxa.

Hybridization has played an important role in the evolution of many groups of the genus *Oenothera*, so that a satisfactory taxonomy often can be worked out only on an experimental basis. In the course of my investigations with hundreds of strains of living plants at the University of Düsseldorf, I was able to ascertain that the most recent revision of subgenus *Raimannia* (Munz, 1935) was inadequate in dealing with the rich pattern of variation in this group. It was soon evident that there were many more distinct entities than had previously been thought to exist; the phenomenon of complex heterozygosity had not been taken into account in earlier efforts to classify the subgenus. In the case of *Renneria*, no revision of the entire group has hitherto been available. In the more recent floristic and taxonomic literature all species have been treated under the names *Oenothera campylocalyx* and *O. rubida*.

The common ancestor of what have been regarded as the subgenera *Euoenothera*, *Raimannia*, and *Renneria* of *Oenothera* almost certainly originated in the semiarid to subhumid regions of western North America in mid-Tertiary time (Raven, pers. comm.). This region is, in fact, the center of evolution of the entire tribe Onagreae, to which *Oenothera* belongs. Geologically speaking, the arrival of *Oenothera* in South America seems to have been very recent, an event of the past several million years (Raven & Axelrod, 1974). Aside from five of the ten species of *Hartmannia* (Raven & Parnell, 1977) and two of *Lavauxia*, all indigenous South American species of *Oenothera* are included in sect. *Oenothera* and are treated in this revision.

Considering the reticulate relationships between the species grouped by Munz (1965) as the subgenera *Oenothera* and *Raimannia*, as well as the complex pattern of relationships among the South American species of this group, it seems preferable to regard all as belonging to a single infrageneric taxon. This taxon is well differentiated from all other groups in the genus, both morphologically and in terms of its crossability. In accordance with the practice established for all other genera of Onagraceae, this group is designated a section, sect. *Oenothera*. The South American species of this section, all but four of which are assigned to the newly described, endemic subsection *Munzia*, are the subject of this revision.

Oenothera sect. *Oenothera* subsect. *Munzia* is regarded as comprising three series and 45 species, of which three are divided into two subspecies each and five others are divided into three subspecies each, for a total of 57 taxa. One or more strains of each of these were cultivated in the experimental garden at the Botanical Institute of the University of Düsseldorf. All plants examined cytologically were diploid, $2n = 14$. The cytological examination of 600 plants representing 280 strains showed that 20 species formed pairs of chromosomes at meiotic metaphase I. All others were complex heterozygotes that formed either a complete ring of 14 chromosomes at meiotic metaphase I or a stable ring configuration (ring of 12 and 1 bivalent; ring of 8 and ring of 6, or ring of 10 and ring of 4).

Many of the species of subsect. *Munzia* vary in such a way that they could be subdivided into several more species if the pattern of distribution of their morphological characteristics were taken as preeminent. In other words, if all of the small differences within the subsection that are preserved by the syndrome of self-pollination and complex heterozygosity, and which have in many cases come to characterize populations, were to be recognized taxonomically, one could recognize literally hundreds of species without any gain whatsoever in taxonomic utility.

There are many direct genetic connections between the South American species recently referred to subg. *Renneria* (Fischer, 1962) or earlier to subg. *Euoenothera* (Munz, 1933) and those referred to subg. *Raimannia* (Munz, 1935). The South American species referred to these two groups are completely interfertile with one another. Judging by the patterns observed, hybridization seems often to have occurred in nature, and at least a dozen species, referred in this monograph to series *Clelandia*, seem to have originated as complex

heterozygotes between these two morphologically quite distinctive groups. The species assigned to this series combine one genome derived from series *Renneria* with another derived from series *Allochroa*. The group is not, however, to be regarded as a transitional one between these two series; no such transition exists. Rather it has originated as a result of hybridization between individual species of *Renneria* and individual species of *Allochroa*, as a result of which the species share a number of characteristics in common. The differentiation of the narrow-fruited ancestors of series *Allochroa* took place first, evidently from plants that resembled those now assigned to series *Renneria*. Presumably this took place at the southern end of the area of distribution of series *Renneria*, which is the region of overlap between the two series at the present time (Fig. 7), and therefore the area in which the species of series *Clelandia* are concentrated. It appears likely that many of the species of this series might have had a very recent origin; with the exception of *O. magellanica* and *O. punae*, each has a restricted area of distribution.

Genetic relationships thus seem to demonstrate a unity between South American species of *Raimannia* and the group that has recently been called *Renneria*. On the other hand, the North American species of *Raimannia*, including *O. laciniata*, do not appear to be closely related to any species of this South American group as its members are to one another, and they are here regarded as comprising a separate subsection *Raimannia*. This group is native only in North America with the exception of the entity that has been called *O. laciniata* subsp. *pubescens*, which ranges south to Colombia, Ecuador, and Peru.

To series *Renneria* (13 species) belong all species with short, urn-shaped capsules, except for one element within the species *Oenothera nana* which was put in sect. *Raimannia* by Munz (1935); see p. 488. Series *Allochroa* (21 species) comprises only a portion of the South American species of *Raimannia*, for which a new name was needed since *O. laciniata* is the type of *Raimannia*. Since the complex connections between *Renneria* and *Allochroa* are now better understood, species of hybrid origin between them, all complex heterozygotes, have been designated as a distinct series here named *Clelandia* (11 species). The species here treated as series *Clelandia* have generally been treated in the literature under the names *O. odorata*, *O. stricta*, *O. indecora*, and *O. nana*.

The species of *Renneria* (in the sense of Fischer, 1962), with their subangular seeds and heavyset capsules, are confined to the high Andes. They probably are close to the ancestral form for the section, and may have subsequently given rise to the other South American groups. The species of series *Allochroa* occur mainly at lower elevations, although some species do extend into the moun-

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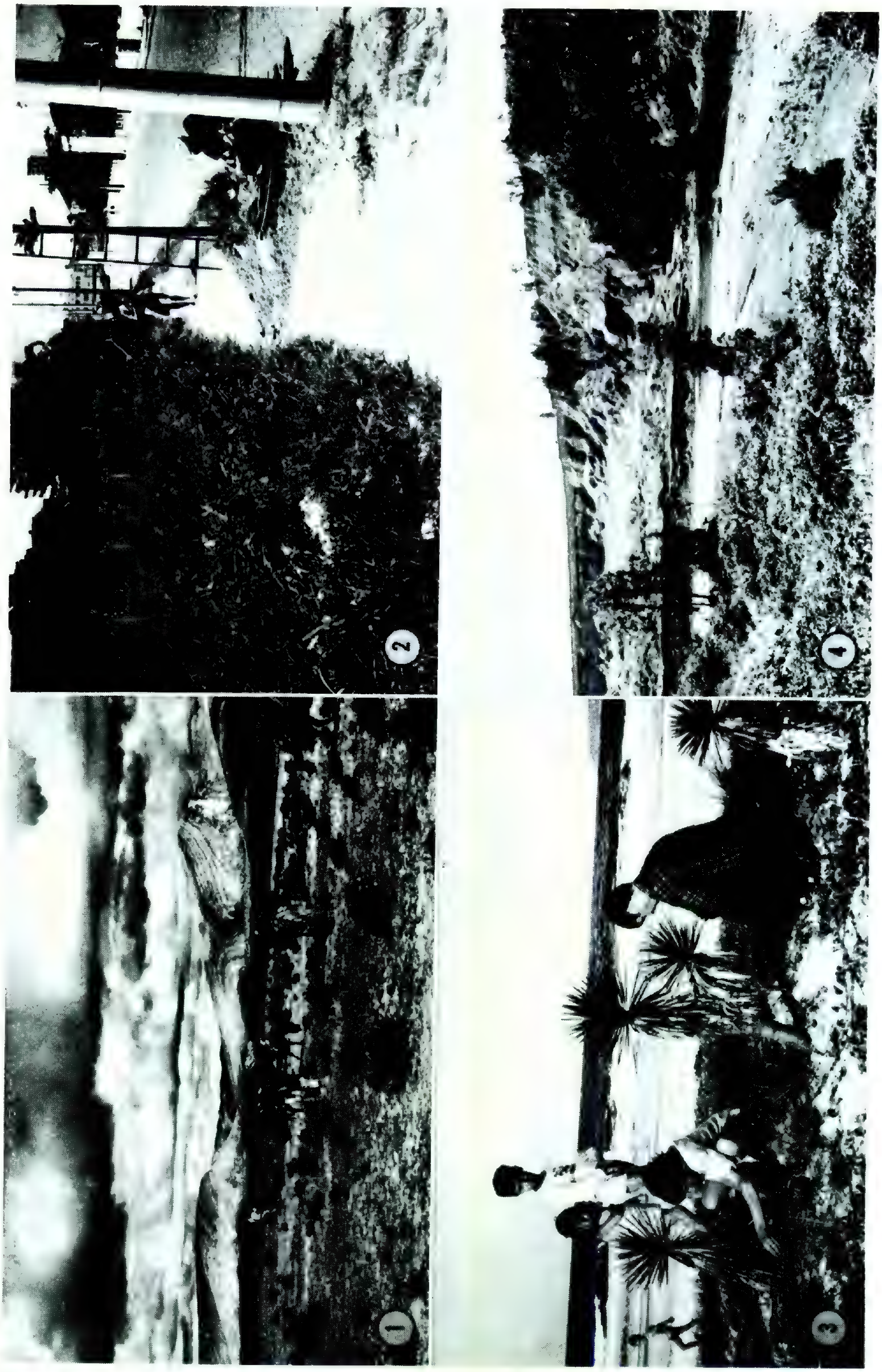
FIGURES 1–4. Habitats of *Oenothera* sect. *Oenothera* taxa in South America.—1. Habitat of *O. nana* and *O. punae*, between Yaví and La Quiaca, 3,500 m, Jujuy, Argentina (Santarius).—2. Habitat of *O. indecora* subsp. *bonariensis*, Itajaí, Santa Catarina, Brazil (Dietrich).—3. Habitat of *O. catharinensis*, Isle of Santa Catarina, Santa Catarina, Brazil (Dietrich).—4. Habitat of *O. stricta* subsp. *stricta* and *O. villaricae*, Río San Pedro near Lago Riñihue, Valdívia, Chile (Stubbe).



tains. In the South American continent, various lines of the section have radiated into habitats ranging from coastal beaches to relatively high elevations. The common ancestor of these groups seems to have reached South America within the past several million years (Raven & Axelrod, 1974). It radiated extensively in South America in relation to the many drastic changes in habitats that occurred in the Pleistocene and more recently (Simpson, 1975). The arrival of *O. laciniata* subsp. *pubescens* in South America was probably an event that occurred considerably later, perhaps only 100,000 years or so ago.

Cytogenetic Basis of Evolution

Just as in North American species of subsect. *Euoenothera*, there occur among the South American members of sect. *Oenothera* species which are chromosomally homozygous and form pairs of chromosomes or small rings at meiotic metaphase I, as well as others which are complex heterozygotes and form a ring of 14 or other large rings at meiotic metaphase I. Some of the plants which are essentially chromosomally homozygous also form small rings which segregate in an alternate fashion at meiotic metaphase I. All of the complex heterozygotes are highly self-pollinating as they are throughout the Onagraceae, with the possible exception of *O. erythrosepala*, whereas the chromosomal homozygotes range from self-pollinating to strongly outcrossing. All homozygotes of subsect. *Munzia* that have been investigated were genetically self-compatible. Most of the complex heterozygote species are true-breeding hybrids which combine genomes from two species which may be very distinct from one another. Their progenies are however uniform; they behave as true-breeding distinct species in nature. On account of the alternate disjunction of the ring of 14 chromosomes in such complex heterozygotes, two sets of 7 chromosomes behave as two different chromosomes when segregating in meiotic anaphase I. In this way the possibility of interchange between the two genomes and consequent segregation is minimized.

Additional aspects of the genetic system, such as lethal factors, genes for self-sterility, and selective fertilization (Arnold, 1962; Schwemmle, 1968) prevent the reconstitution of the homozygotes at least in a viable form. Following self-fertilization, which is the rule in the complex heterozygotes, or outcrossing with another similar individual of the same population, the complex heterozygote is always reconstituted. Only in exceptional cases does one of the chromosomally homozygous parental types segregate in the progeny of a complex heterozygote, as discussed under *O. acuticarpa* on p. 606.

Cleland (1972: chap. 7) has given a plausible explanation for the origin of the rings of 14 chromosomes which occur in complex heterozygotes of *Oenothera*. The rings are formed because of reciprocal translocations between nonhomologous chromosome arms. Such reciprocal translocations, which probably occur at a low frequency in all groups of organisms but become a regular part of the adaptive system in only a few, do not lead to an unequal distribution of the chromosomes to the poles in *Oenothera* because of regular alternate disjunction of rings of chromosomes in this genus. All of the chromosomes are the same length, have

FIGURES 5–6. Habitats of *Oenothera* sect. *Oenothera* taxa in South America (continued). —5. Habitat of *O. santarii*, Cerro los Gigantes, 2,000 m, Sierra Grande, Córdoba, Argentina (Dietrich).—6. Habitat of *O. ravenii* subsp. *ravenii*, San Bernardino, Lake Ypacaraí, Cordillera, Paraguay (Dietrich).

arms of equal length, and appear euchromatic only at the end segments; this structure may facilitate alternate disjunction in the rings (Kurabayashi et al., 1962). Similar translocations between dissimilar nonhomologous chromosomes would lead to a high percentage of misdivision and therefore to a degree of sterility in the plants in which they occurred.

In the evolution of the genus *Oenothera* the phenomenon of reciprocal translocation has played a decisive role. Following self-pollination or crossing of plants with small rings of chromosomes, it is possible to observe in the progeny not only chromosomal homozygotes which form 7 bivalents structurally identical to the original form of the species but also others which differ from the original form in the arrangement of their chromosome arms. Such plants constitute the starting point for the origin of new complex heterozygote species in the genus *Oenothera*. Through the hybridization of homozygous strains with others with a sufficiently different end arrangement, a ring of 14 or other stable configuration may arise, and then we can speak of permanent structural heterozygosity.

In contrast to the North American species of subsect. *Euoenothera*, there are among the South American species many homozygous ones in addition to a rich

array of complex heterozygotes. Since all complex heterozygotes are by definition capable of being traced back to a homozygous original form, we have attempted in the course of our work to synthesize existing complex heterozygotes through hybridization between existing chromosomally homozygous species when possible, and by crossing such complex heterozygotes back to their putative parents to illuminate the nature of the chromosomal complexes contained in them.

It was possible to make a very comprehensive analysis of the complex heterozygotes in this group owing to the virtually unrestricted crossability of all species of this section. Fortunately, all of the genomes represented in the complex heterozygotes among the South American species are still represented in homozygous combinations among other species of the group. This should not be taken to infer that the phenotypes of these homozygous species are absolutely identical with those of the strains which originally gave rise to the complex heterozygotes, however, for many genomes have during the time they were combined in such complex structural heterozygotes become altered to a certain degree.

Although *Oenothera* does have an unusual genetic system, hybridization may play no greater a role in the origin of new species in this genus than it does in many groups of higher plants (e.g., Ehrendorfer, 1971). Only in the exact method of origin of the complex heterozygotes, which may perpetuate intermediate hybrid phenotypes, do they differ strikingly from methods of the origin of species through hybridization found in other groups of plants.

Distribution and Phylogenetic Relationships

The general range of the South American species of this group and of the individual series is shown in Fig. 7. Especially notable is the extensive zone of overlap between *Renneria* and *Allochroa* as well as the frequency of chromosomally homozygous species of both subsections in the vicinity of the Cordillera Oriental of Argentina. In addition, most species of the entirely hybrid series *Clelandia* occur in this area. The occurrence of so many species of both groups, and of the intermediates between them, in this particular region is probably related to the very close genetic relationship between *Allochroa* and *Renneria*, plants similar to the latter group having probably given rise to the original members of series *Allochroa* during the past.

Rapid evolution of the species of the two groups in this region has no doubt been made possible in part by the rich diversity of habitats found in a relatively limited area along the east side of the Andes. Moreover, because of the impenetrable tropical forest and of the Gran Chacó, it is not surprising that the first migration out from the region of the Cordillera Occidental occurred towards the east and southeast into the open plains of Argentina. From here, secondary migration eventually resulted in the colonization of Paraguay, Uruguay, and southern Brazil. Ultimately members of this group migrated by way of the Andean passes to Chile.

Species of series *Renneria* occur outside of the Andes only in the highest elevations of the Sierra Grande and the Sierra de Comechingones. Only their derivatives in which the characteristic phenotype of series *Allochroa* was evolved

FIGURE 7. Areas of the three series of subsect. *Munzia*: ser. *Renneria*, vertical lines; ser. *Allochroa*, horizontal lines; ser. *Clelandia*, diagonal lines.

were able to colonize the plains and eventually reach the seacoast. The species of series *Renneria* have remained strictly adapted to the high mountains.

In Fig. 7 it can also be observed that the combination of genomes from series *Renneria* with those from series *Allochroa*, resulting in the origin of the entirely complex heterozygotes of series *Clelandia* resulted in plants which were able to greatly extend the area of the two parental series. On the one hand, series *Renneria* was able to penetrate to the southernmost point of the continent of South America at Punta Arenas only in the combination *Oenothera magellanica*, while on the other hand series *Allochroa* was able to penetrate to high elevations in the mountains of southern Peru only in the combination known as *O. punae*.

Figure 8 is a plausible phylogenetic scheme for the evolution of series *Allochroa* from *Renneria*. *Oenothera odorata* and *O. mendocinensis* were derived from a plant which probably resembled the present day *O. santarii*, and they have remained confined mainly to the southern regions of South America. On the other hand, *O. ravenii*, *O. longiflora*, *O. indecora*, and *O. affinis* have extended their ranges mainly to the east. *Oenothera ravenii* and *O. longiflora* may have belonged to a group which developed around plants with a phenotype somewhat like that of *O. longituba*; *O. indecora* and *O. affinis* seem to be more closely related to a plant with the phenotype of *O. scabra*. *Oenothera catharinensis* seems to have been derived from *O. ravenii* as an obligate annual of local distribution. *Oenothera verrucosa* with *O. coquimbensis* and *O. featherstonei* seem clearly to have been derived earlier from plants similar to those of series *Renneria*, and independently from those species mentioned above of series *Allochroa*.

Even though Munz (1935) put the taxa here regarded as series *Allochroa* and *Raimannia* into the same subgenus, it is difficult to establish any direct connection between them. On the other hand, there is a close and demonstrable relationship between the species of *Allochroa* and those of *Renneria*, treated by Munz (1935) as comprising separate subgenera. Their relationship is demonstrated by the fertility of almost any hybrid combination and even more strongly by the compatibility of their plastids. The hybrids between *Renneria* and *O. indecora*, *O. mendocinensis*, and *O. odorata* suggest that these species may be closest to *Renneria*, since they are capable of becoming fully green in both directions. In addition, albino or variegated plants have not been observed to occur among hybrid progenies involving these species with one another. In contrast, there are significant differences between the plastids of subsect. *Raimannia* and those of subsect. *Munzia*: hybrids between *O. laciniata* subsp. *pubescens* and species of *Munzia* were albino or very light green and set seed poorly (unpublished; Stubbe, pers. comm.).

There appears to be full plastome compatibility within the taxa of series *Renneria*, since all hybrids I have observed thus far were fully green. The establishment of differentiated plastome types seems to have taken place within subsect. *Munzia* only after the evolution of series *Allochroa* from *Renneria*. According to present information based on hybrids I have examined, it appears that *O. affinis*, *O. longiflora*, and *O. ravenii* each has its own distinctive plastid type.

FIGURE 8. Phylogenetic scheme of the evolution of *Oenothera* subsect. *Munzia*.

If this is the case, there would be at least four different plastid types within series *Allochroa*. Our investigations concerning the representation of these four plastid types among the complex heterozygotes are incomplete, and it is not possible to make a definitive statement about this matter at present.

Unlike the situation among the North American species of subsect. *Euoenothera*, distribution of the chromosomally homozygous forms in South America seems to have remained approximately as wide as that of their complex heterozygote derivatives, at least in series *Renneria* and *Allochroa*. Only in the cases of *O. peruana*, *O. santarii*, *O. ravenii*, and *O. longiflora* does it seem likely that the present area of distribution represents only a remnant of an earlier and much wider distribution. In addition, the ranges of *O. verrucosa* and *O. featherstonei* might be regarded as relictual.

Whole series of species of *Renneria* and *Allochroa* seem to have acquired the ability to greatly extend their ranges of distribution, in a sense, by forming new complex structural heterozygous combinations with other species. From this it can be assumed that the ability of these complex heterozygotes to colonize new areas is greater than that of the corresponding homozygotes. This seems to be especially clear with respect to Chile, where only complex heterozygous species of subsects. *Allochroa* and *Clelandia* occur, except, of course, for the occurrence of *O. coquimbensis* in the deserts of the far north.

In the course of their migrations the complex heterozygotes seem often to have migrated by a circuitous path, as can be illustrated especially clearly by the history of the *O. odorata* complex. The *odorata*-complex first of all participated in the origin of *O. stricta*, the other parent being *O. ravenii*. *Oenothera stricta* is now very widespread and abundant in Chile. Figures 241–244 show other examples of the spread of different complexes.

Analysis of Complexes

The analysis of complex heterozygotes in Düsseldorf was made possible by the comparison of various artificially produced complex heterozygotes with naturally occurring ones. In addition, naturally occurring complex heterozygotes were hybridized with their putative chromosomally homozygous parents in both directions, and the hybrids evaluated morphologically. The association of chromosomes was of no value in most cases in assessing the relative parentage of the different forms. Haustein (1952) pointed out over 20 years ago that chromosomal pairing was of almost no value in determining phylogeny in this group, as it was always complete and variable within many species.

If, for example, a hybrid between a randomly chosen line of *Oenothera versicolor* and one of *O. scabra* formed 7 bivalents, one could certainly conclude that these two strains are related to one another, since the pairing of their chromosomes is undisturbed, and fertility, whether measured by pollen or seeds, is complete. About the degree of relationship between them, however, relative to other species of the group, this test says nothing. In many instances, the evolution of species within series *Renneria* especially seems to have taken place solely by genetic changes, not involving any rearrangement of chromo-

some structure. As another example, I might mention that "*longiflora* Erlangen," a strain of *O. affinis* (series *Allochroa*), gave a hybrid with a ring of 4 and 5 bivalents when crossed with a strain of *O. scabra* (*Santarius 2003*; series *Renneria*) collected in Bolivia. These structural homologies cannot be taken as a strong indication of a particular relationship between *O. affinis* and *O. scabra*, however, since within *O. affinis* itself, hybrids have been observed to form configurations at meiotic metaphase I ranging from 7 bivalents to a ring of 14.

Other indications that chromosomal configurations in hybrids between various South American species are not a useful index to relationship is provided by the following observations. Even in individual populations of *O. affinis* and *O. odorata*—populations which appear morphologically homogeneous—there may be found individuals forming 7 bivalents, others which form a ring of 14 at meiotic metaphase I, and still others with smaller rings. In short, chromosomal evolution does not seem to have proceeded among this group of species at the same rate as morphological evolution, and the two do not appear to be highly correlated. Variation of this sort has been found in limited areas; for example, *Santarius 1869* represents a sample that in the experimental garden was morphologically indistinguishable from *Santarius 1850*, and both were referable to *O. affinis*. When hybridized, these two populations yielded progeny in which the plants formed a ring of 14 at meiotic metaphase I. On the other hand, when plants from *Santarius 1869* were hybridized with a morphologically very distinctive strain with broad leaves from 1,600 km away—*Santarius 193*—they formed a ring of 4 and 5 bivalents. When they were hybridized with *Santarius 1711*, another strain of *O. affinis* from about 350 km away, they formed a ring of 6 and 4 bivalents.

Oenothera affinis is evidently in a stage of evolution in which the chromosomal homozygotes are more widespread and much better represented than the heterozygotes. The sorts of intermediate chromosomal configurations that occur frequently indicate, however, that a wide variety of different end arrangements occurs in the species. In cultivation, the complex structural heterozygotes breed true and do not "throw off" homozygous derivatives.

This pattern is very different from that worked out by Cleland (summary in Cleland, 1972) for the North American subsect. *Euoenothera*. On the basis of his studies of this group, Cleland worked out a theory whereby the accumulation of reciprocal translocations within a population, accompanied by geographical isolation, would lead eventually to the origin of populations which were essentially chromosomally homozygous but characterized by different end arrangements. If these strains eventually spread and came into contact, complex heterozygotes might originate in a single step by hybridization in the zone of contact. These complex heterozygotes, fixed from their origin, would breed true and would eventually replace the chromosomal homozygotes with which they occurred.

A situation similar to that just described for *O. affinis* can be accepted for *O. odorata*. With respect to its chromosomal configurations, *O. odorata* is extremely variable. Plants with 7 bivalents and all configurations up to and in-

cluding complex heterozygotes with a ring of 14 occur. From this, it can be concluded not only that a variety of differentiated chromosomally homozygous types occur within the species, but also that the species is still in a state of active evolution chromosomally. It is not clear whether the complex heterozygotes within this species have formed through hybridization between chromosomal homozygotes completely differentiated with respect to their end arrangements, or have accumulated following the formation of rings of chromosomes of intermediate size by further spontaneous reciprocal translocation. In some populations, the balance seems to have shifted definitively toward a preponderance or exclusive representation of chromosomal structural heterozygotes, while in others, chromosomal structural instability seems to be the rule. In the vicinity of Comodoro Rivadavia, Prov. Chubut, the essentially stable configuration of a ring of 12 and 1 bivalent seems to have become predominant.

Results such as those discussed for *O. affinis* and *O. odorata*, lead to a view of the origin of complex heterozygosity quite different from that presented by Cleland and others for subsect. *Euoenothera*. In these South American species, as in some others, chromosomal structural heterozygotes occur together with homozygotes and plants with intermediate configurations in the same populations. There is evidently no direct correlation between the formation of strains or populations that are well differentiated either genetically or phenotypically and the origin of complex heterozygosity, since in these cases the only major difference between the genomes represented in the heterozygotes seems to be that concerning the actual end arrangements represented. It seems unimportant whether the pattern of end arrangements responsible for the ring of 14 arose gradually or in a single step.

Oenothera affinis, like all other South American species of the section, is self-compatible and often self-pollinating, the anthers shedding pollen directly on the stigma at anthesis. Therefore, regardless of how a complex heterozygote originates, it would tend to persist in the population alongside plants with other chromosomal configurations owing to regular self-pollination.

This species exhibits several stages of complex heterozygosity. The first, in which homozygotes still segregate from the heterozygotes, is not known in *O. affinis*, although it does occur in *O. acuticarpa*. In the second stage, the complex structural heterozygotes are plants with large flowers and a long floral tube, indistinguishable from chromosomal homozygotes of the same species. The population of *O. affinis* in Chile is probably nearly or quite dominated by complex heterozygotes. However, only one bit of actual cytological information is available (Stubbe in 1961). Examination of the pollen of plants from four populations from the provinces of Atacama, Coquimbo, and Valparaíso (*Johnston 5860*; *Behn 8468*, *22798*; and *Eyerdam 10040*) revealed from 20–35% empty grains, however. A fifth population, from Aconcagua (*Behn 22802*), had essentially no empty grains, which makes it virtually certain that it was chromosomally homozygous. The origin of complex heterozygosity in the Chilean populations seems to have been very recent, and it may be that the original plants that became established on the west side of the Andes were already heterozygotes.

The third phase in the evolution of complex heterozygosity occurs when all plants are small flowered and self-pollinating, although retaining the long floral tube characteristic of *O. affinis*. Further reduction of flower size would lead eventually to plants with a short floral tube also, as has occurred in the evolution of *O. mollissima* from *O. affinis*. The morphological changes that have occurred in *O. mollissima* have been so extensive that it is best regarded as an independent species at the present time (Hecht, 1950; Hecht & Tandon, 1953). Even though these species often occur in mixed populations, the regular self-pollination of *O. mollissima* seems to constitute an effective and sufficient barrier to interspecific hybridization in nature; hybrids occur only occasionally.

The origin of complex heterozygosity in *O. elongata* (series *Clelandia*), in contrast to the situation discussed in *O. affinis* and *O. odorata*, involved hybridization between two distinct taxa. Other clear-cut examples of this sort of evolutionary process are afforded by the origin of *O. magellanica*, *O. siambonensis*, *O. stricta*, and *O. villaricae*. The strain of *O. elongata* from the province of Catamarca (Diers in 1959) has had a remarkable history, quite apart from the fact that the locality is far from the main area of distribution of the species. In 1960, an individual plant appeared in the progeny of a seed sample from *O. longituba* at the same locality, gathered in the wild. In all probability, this plant was a spontaneous hybrid between *O. longituba* and *O. affinis*, both of which commonly grow together in Catamarca. On self-pollination, however, it bred true, and it has now been maintained in cultivation for 13 years as a complex heterozygote, without showing any tendency to segregate the characteristics of its presumed parents. The original plant gave evidence of plastid incompatibility and probably would not have been vigorous enough to survive in the wild; by a fortunate chance, it was grown in the experimental garden to give clear evidence of the mode in which a particular complex heterozygote could have been formed. Evidently the one-step, efficient formation of this chromosomal arrangement deterred the segregation of the parental species from the start.

Spontaneous hybrids with *O. affinis* also appeared in the progenies of two other collections of *O. longituba*, *Santarius 1736* and *1737*. These had intermediate chromosomal configurations, however, of a ring of 6, a ring of 4, and 2 pairs; 2 rings of 6 and 1 pair; and a ring of 12 and 1 pair, and probably would not have been stable as was the plant discussed above and assigned to *O. elongata*.

Two principles seem to have been important among the evolution of different South American species of this group. In some species extensive genetic changes have taken place without structural modifications of the chromosomal end arrangements. Thus, the strains of *O. peruana*, *O. versicolor*, and *O. scabra* that have been grown in the experimental garden have been chromosomally structurally identical. Other species of series *Renneria* have not deviated far from this chromosomal structural arrangement either, so that a ring of 4 and 5 bivalents was formed both in hybrids between *O. santarii* and *O. versicolor* and also in hybrids between *O. pedunculifolia* and *O. versicolor*.

In many other species structural changes in the form of reciprocal translocations have played a definitive role in the differentiation of species. These

translocations have not led to a reduction in fertility because of the regular alternate disjunction of the chromosomes in the rings. As a result, a whole array of chromosomally distinctive lines has arisen from such events. Familiar isolating mechanisms of a geographical, ecological, or physiological nature have in many instances allowed complete speciation following or accompanied by such chromosomal differentiation. In the absence of barriers to hybridization between chromosomally differentiated lines within the group, many such lines have eventually hybridized to produce new complex heterozygous combinations. Indeed, identical combinations have been found, evidently formed more than once at different times in different places. Examples of this are provided by *O. stricta* and *O. picensis*, and these are discussed further under the treatments of the respective species.

As in the chromosomal homozygotes, genetic changes that have occurred in the complex heterozygotes have led eventually to a still further differentiation. The tendency towards the evolution of small-flowered plants in which self-pollination is more and more automatic, regarded in this paper as the ultimate phase in the development of complex heterozygosity, is unmistakable. Despite the extensive suppression of crossing-over in *Oenothera*, the occasional exchange of genes between complexes seems to have had an effect on the course of evolution. An example of this, *O. elongata*, with complexes derived from *O. longituba* and *O. affinis*, has been mentioned. Hybrids between this complex heterozygote and *O. affinis* have shorter capsules than *O. affinis* and this characteristic of *O. longituba* seems to have been introduced by gene exchange in the complex heterozygote. In contrast, *O. picensis* (*Santarius 1549*) is clearly made up of more or less unaltered *O. affinis* and unaltered *O. odorata*. Also, *O. villaricae*, which is known as "*berteriana* Erlangen" in the genetic literature and belongs to series *Clelandia* can be shown to be made up of complexes derived from *O. santarii* and *O. ravenii*.

Among the additional factors of phylogenetic importance among the South American species may be mentioned complex heterozygosity involving more than two species (see species numbers 12, 16c, and 28). A very curious phenomenon involving *O. nana* and *O. punae*, involving a situation in which freely recombined genomes at a single locality seem to be unequally shared by both species, is discussed on p. 611.

An important result of this study is the conclusion that the origin of complex heterozygosity does not depend upon the prior existence of genetically well-differentiated genomes. It can be shown, especially in *O. affinis*, that chromosomally very well-differentiated forms can occur within a single population, be preserved by self-pollination, and eventually give rise to complex heterozygotes which are morphologically essentially identical to the chromosomal homozygotes at that place. (See also Drillisch, 1975: 60–71.) Such complex heterozygotes, since they are from the beginning self-pollinated, may immediately be more or less isolated from other elements of the population and thus in effect give rise to a new and distinctive strain. Thus rings of 14 can arise in a variety of ways in populations of *Oenothera*, either through the hybridization of chro-

mosomally and genetically very well-differentiated strains, or through the gradual accumulation of differences, even within populations.

In contrast to the species of the North American subsect. *Euoenothera*, chromosomal homozygotes are still very well represented among the South American species, even though complex heterozygotes are likewise frequent. These chromosomal homozygotes still have ranges as extensive as those of their complex heterozygous derivatives, and often occur together with them in the same areas (Table 1). The analysis of the South American complex heterozygotes is facilitated by the existence of all of the original participating homozygotes at the present time. The various mechanisms operative in the differentiation of species all can still be observed directly at the present day.

In very actively evolving groups, such as the species of *Oenothera* in South America which are treated in this paper, it is often not possible to delimit sharply defined natural units. Almost all complexes of series *Renneria* and *Allochroa* are interconnected with one another, and they are in a very real sense evolving as an interconnected whole. Connections between species, taken step by step, unify the most distantly related and distictive elements in the group into an intertwined complex of great intricacy but presumably also great evolutionary vigor in responding to the demands of the environment. The two most important elements in the evolution of the group, however, appear to be complex heterozygosity and hybridization. This seems to be particularly true among the South American species of *Oenothera* because of the complete lack of sterility barriers, and because of the chromosomal system which leads easily to the formation of true-breeding hybrids which recombine the characteristics of the parents in various adaptative ways. The frequent instances of sympatric occurrence of the various taxa, with consequent opportunities for hybridization, is documented in Table 1.

In fertile, pair-forming hybrids such as are encountered in many groups of plants, adaptive phenotypes may soon be broken up by recombination and backcrossing, but in stable hybrids, such as self-pollinating complex heterozygotes, it may be preserved. Once a successful complex heterozygote has originated, it may spread in areas beyond those occupied by its homozygous parents, owing to its different adaptive mode, and eventually the parental homozygotes may come to exist only in relatively limited areas, as in the North American subsect. *Euoenothera*.

Systematic Treatment

Before commencing the formal taxonomic treatment of the South American species of this group, I would like to make a few comments about the descriptions and the way I have employed terminology in them. For the descriptions of individual pubescence types the terms strigillose, villous and glandular-pubescent have been used. All hairs are fundamentally single-celled. "Strigillose" is used to designate short, appressed hairs about 0.1–0.2 mm long; "villous," hairs which stand erect or rise obliquely and are 1–5 mm long; and "glandular-pubescent," hairs 0.1–0.3 mm long which are terminated by a gland. Shorter and appressed

TABLE 1. Sympatric occurrence of taxa of native South American taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.

		peruana	versicolor	lasiocarpa	santarii	longituba	tafien taf	pedunculif	scabra	rubida	tarijensis	recurva	sandiana	nana	mendocinen	odorata	raveni rav	raveni arg	raveni chi	longif gra	longif lon	catharinen	indeco ind	indeco bon	affinis	mollissima	rivadaviae	strict str	strict alt	strict arg	bahia-blan	picens pic	picens cor	picens bon	monteviden	pseudolong	parodi par	parodi str	parodi bra	verrucosa	coquimbens	arequipens	grisea	feathersto	nocturna	magellanic	villaricae	elongata	pseudoelon	cordobensi	siambonens	brevipetal	aculicarpa	tucumanens	punae	lacini pub
REN	peruana									●																														●																
	versicolor			●		●	●	●	●		●	●	●	●												●																								●	●				●			●	
	lasiocarpa		●			●	●	●	●						●											●																															●	
	santarii						●									●										●																					●					●					
	longituba		●	●			●	●	●						●											●																										●		●		●	
	tafien taf		●	●	●	●		●	●						●											●																					●				●	●		●		●	
	pedunculif		●	●		●	●		●						●											●																										●		●	●	●	
	scabra		●	●		●	●	●			●	●	●	●												●																						●	●		●		●		●	
	rubida	●																																						●																
	tarijensis		●						●			●	●	●												●																						●								●	
	recurva		●						●		●		●	●												●																						●								●	
	sandiana		●						●		●	●		●																																		●	●						●	●
	nana		●	●		●	●	●	●		●	●	●																																			●								●	
ALL	mendocinen															●								●	●		●			●	●	●	●	●			●	●								●										
	odorata				●										●			●									●		●	●	●	●		●				●								●										
	raveni rav																				●		●	●	●	●									●		●		●																	
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	raveni chi																											●																		●									
	longif gra																				●		●	●	●												●		●																	
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	catharinen																																																							
	indeco ind																●	●		●	●			●	●	●							●		●		●		●																	
	indeco bon														●		●	●		●	●		●		●	●				●			●		●	●	●		●															●		
	affinis		●	●	●	●	●	●	●		●	●			●		●	●		●	●		●	●		●		●		●		●	●		●	●	●		●		●		●			●		●		●	●		●	●	●	
	mollissima																●	●			●		●	●	●									●	●	●	●		●																	
	rivadaviae														●	●																					●									●										
	strict str																		●						●							●									●		●			●	●									
	strict alt															●																														●	●									
	strict arg														●	●		●						●	●								●	●			●	●																	
	bahia-blan														●	●		●																●			●	●								●										
	picens pic														●	●									●			●				●									●		●			●										
	picens cor														●			●					●	●	●					●							●									●				●						
	picens bon														●	●		●							●				●	●						●	●																		
	monteviden																●	●			●		●	●	●	●											●		●																	
	pseudolong																				●			●	●	●																													
	parodi par														●		●	●		●	●		●	●	●	●	●			●	●		●	●	●			●	●											●				●		
	parodi str														●	●		●											●	●			●			●																			
	parodi bra																●	●		●	●		●	●	●	●									●		●																			
	verrucosa	●								●																																														
	coquimbens																								●			●				●											●													
	arequipens																																											●	●											●
	grisea																								●			●				●									●															
	feathersto																																								●			●												●
	nocturna																																								●		●													●
CLE	magellanic				●		●								●	●									●		●	●	●		●	●	●														●			●	●					
	villaricae																		●									●	●																●										
	elongata		●						●		●	●	●	●												●																														
	pseudoelon		●						●				●																																						●				
	cordobensi						●																		●							●				●									●										
	siambonens				●	●	●	●	●																●																				●						●	●		
	brevipetal		●																																												●							
	aculicarpa					●	●	●	●																●																								●			●		
	tucumanens							●															●	●											●													●		●			
	punae		●	●		●	●	●	●		●	●	●	●												●																														
RAI	lacini pub												●																												●		●	●											

villous pubescence is likewise encountered among the South American species of *Oenothera*. All three pubescence types may be present on a single plant.

Description of the form of the vegetative leaves and petals, as well as that of the outline of the buds, capsules, and seeds follows the terminology given by Stearn (1956). Measurements for the buds are given for those just about to open. The length is given exclusive of the floral tube. Measurements of the sepals are given at the same stage. Length of the ovary is given at the stage when the flowers have just opened.

The asterisks on the chromosomal configurations mentioned at the end of the description correspond with those given in the lists of plants cultivated in the experimental garden at Düsseldorf.

The geographical distributions are in general given in broad terms, since many of the ranges, especially those involving the species occurring in the high

mountains, are insufficiently known. Further sampling will be necessary before they can be specified more precisely.

Finally, it is important to add a word about the duration of the plants. Often in the literature and on the labels of specimens, plants of this group are said to be "perennial." In most instances I have not been certain how to treat these observations, since in our experience all species appear to be either biennial (especially the rosette-forming ones) or annual. Probable exceptions, and species that may truly be perennial, are *O. nana* and *O. punae*. I have not been able in any case to find on a herbarium specimen any plant parts indicating that the individuals had flowered more than once, or structures such as overwintering buds which might have indicated a true perennial habit. Structures which might have seemed to have been formed during an earlier flowering cycle could in all cases be attributed to the activities of sheep or other grazing animals. There seems to be no indication that any of these plants are generally perennial, although when they are cropped off by an animal or cut back in a stage of active growth, new shoots will often form freely from the base and a second flowering will take place within the same season. In Düsseldorf we often employed this device in order to synchronize the blooming of two different species which might not otherwise have flowered at the same time.

OENOTHERA sect. *OENOTHERA*

Three subsections are represented in South America, and may be separated by the following key:

1. Seeds prismatic; infrequent naturalized plants .... C. Subsect. *Euoenothera* (p. 615)
1'. Seeds not prismatic; mostly native.
  2. Buds nodding or floral tubes of the oldest buds curved upward .... B. Subsect. *Raimannia* (p. 612)
  2'. Buds erect, the floral tubes not curved upward .... A. Subsect. *Munzia* (p. 443)

A. Subsection MUNZIA

Oenothera sect. **Oenothera** subsect. **Munzia** Dietrich, subsect. nov.

Plantae annuae vel biennes, erectae vel prostratae, rosulares vel erosulares; gemmae non nutantes, tubus floralis non sursum curvatus. Habitat in America Meridionalis.

Annual or biennial plants, erect or prostrate, forming a rosette or growing directly from seed without one, or remaining permanently and flowering as a rosette. Plants unbranched or with a branched main stem and decumbent, arching, or straight side branches arising from the rosette, a few cm to 2 m tall. Rosette 5 cm (*O. nana*) to 70 cm (*O. longituba*) in diameter. Main stem 0.3–2 cm thick. Plants (1) very densely to sparsely strigillose and thickly to sparsely appressed to erect long-villous; (2) very densely to sparsely strigillose, densely to sparsely long-villous, and very sparsely to sparsely glandular-pubescent; (3) very densely to very sparsely appressed or erect long-villous, densely to very sparsely glandular-pubescent; or (4) densely short-villous and glandular-pubescent. Rosette leaves linear, elliptic, or oblanceolate, long or short acute, gradually narrowed to the petiole or sessile, attenuate to acute at the base, 2.5–35 cm long, 0.2–6 cm wide; cauline leaves linear, elliptic, lanceolate, or oblanceo-

late, acute, sessile, acute to truncate at the base, or distinctly short-petiolate and narrowly cuneate at the base, 2.5–25 cm long, 0.1–4 cm wide; bracts linear, elliptic or lanceolate to ovate, acute to almost obtuse, sessile and acute to subcordate at the base or distinctly short-petiolate and attenuate at the base, 1–12 cm long, 0.1–3 cm wide, longer or shorter than the capsule they subtend or ± the same length; leaves regularly or irregularly to sparsely toothed, the teeth obtuse or acute, plane or undulate, the surface sometimes flecked wih black (*O. nana*). Inflorescence simple or branched, dense or rather sparse. Floral tube 0.5–12 cm long, sometimes flecked with red or reddish brown. Buds oblong, elliptic to rotund or lanceolate to ovate in outline, 0.4–3.5 cm long, 0.15–1 cm thick, often red striped at the junction of the sepals or also along the midribs of the sepals. Sepals green or yellow to greenish yellow, often flushed with red, sometimes flecked with dark red or reddish brown; sepal teeth 1–4 mm long, erect or divergent. Petals broadly elliptic or obovate to broadly obovate, rotund or retuse, 0.5–4.5 cm long, yellow to straw colored, sometimes flushed with red near the base and along the nerves, or completely red. Anthers 0.2–1.5 cm long, yellow, sometimes reddish. Filaments 0.2–2.5 cm long, yellow, sometimes reddish. Style 1–14 cm long, surrounded by the anthers in bud or exceeding them in length. Stigma lobes 4, 1–10 mm long. Ovary 0.8–1.5 cm long, cylindrical. Capsule ovate or oblong in outline, narrowed toward the apex, occasionally swollen below the apex (*O. affinis*), fused with the subtending bract at the base or free, occasionally clearly stalked (*O. verrucosa*), erect and appressed to the stem or spreading sharply or even at a right angle to it, 1–6 cm long, 2–10 mm thick; valves of the capsule separating from the placenta when ripe, spreading or curving inward or outward. Seeds 0.8–2 mm long, 0.5–1 mm thick, ± bluntly angled or elliptic to rotund in outline, light brown to dark brown or black, sometimes dark flecked. Self-compatible and outcrossed or self-pollinated. Chromosomally homozygous or permanently heterozygous and isogamous or semiheterogamous. Gametic chromosome number, $n = 7$ (7 bivalents, ring of 14, or intermediate configurations at meiotic metaphase I).

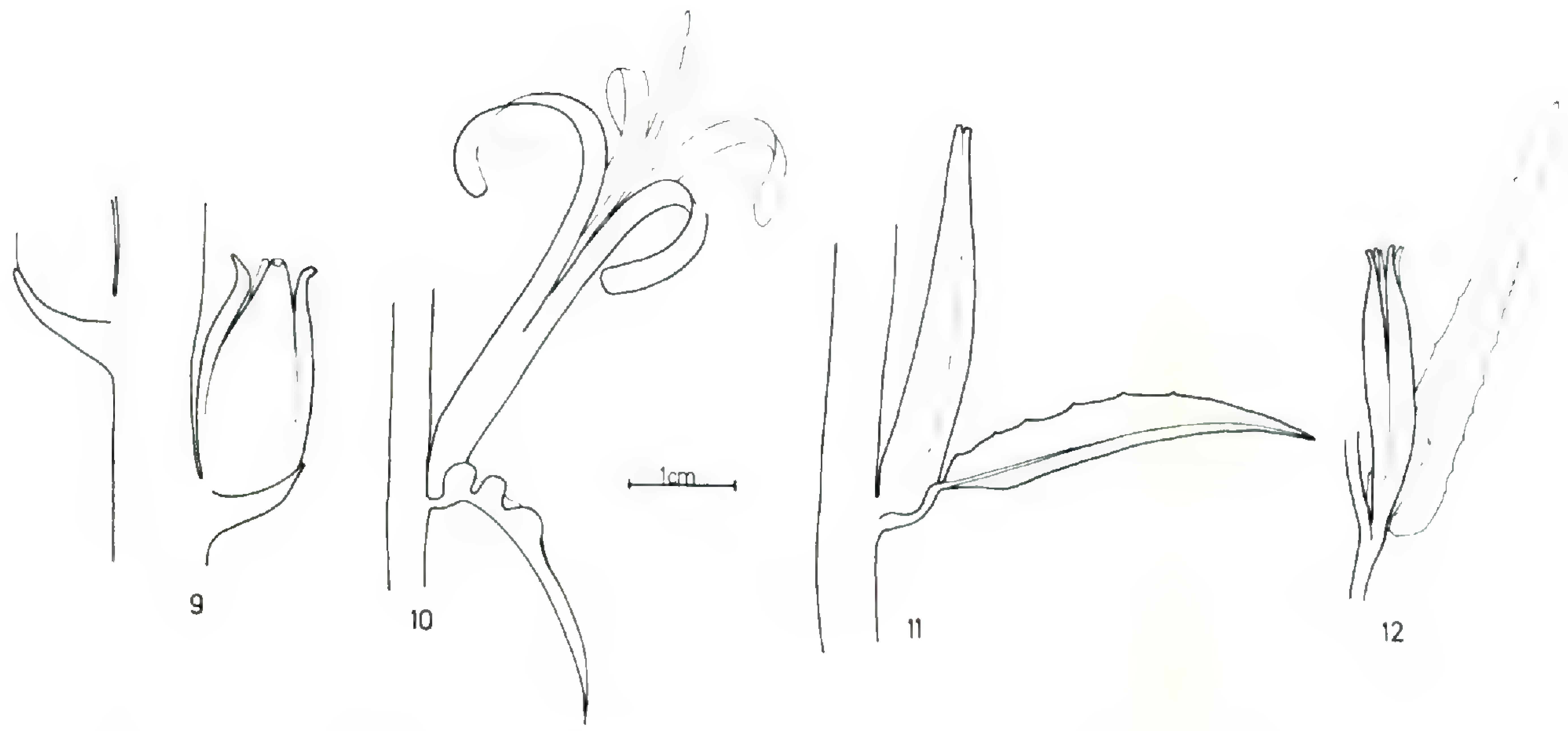
Type species: *Oenothera odorata* Jacq.

Distribution (Fig. 7): All species occur in more or less open plant communities from sea level to almost 5,000 m elevation in the Andes (*O. nana*). Among the sorts of places they grow are seacoasts, dunes and other sandy places, gravelly fields, dry watercourses; fields, meadows, and pastures; open shrublands and woods; grassy and shrub-steppes, Andean puna; banks of streams; edges of roads and disturbed places. The subsections occur nearly throughout the southern half of South America, and northward along the Andes to Colombia; some of its species are widely cultivated and naturalized on other continents.

This subsection is dedicated to P. A. Munz (1892–1974), lifelong student of Onagraceae.

KEY TO THE SERIES OF SUBSECT. *Munzia*

1. Capsule urn-shaped (Fig. 9), gradually narrowed toward the tip, erect or standing out at a right angle from the stem, 4–9 mm thick at the base and with the subtending



FIGURES 9–12. Capsules representative of the series of *Oenothera* subsect. *Munzia*.—9. *O. scabra* subsp. *scabra* (*Renneria*).—10. *O. rivadaviae* (*Allochroa*).—11. *O. acuticarpa* (*Clelandia*).—12. *O. verrucosa* (*Allochroa*).

leaf distinctly fused to it; valves of the capsule spreading after seeds are shed .... Series *Renneria* (p. 450)

1′. Capsule ± cylindrical (Figs. 10–12), at most tapering toward the apex, erect or standing out from the stem, 1.5–4 mm thick, usually not or slightly fused with the subtending bract; valves of the capsule spreading or curved inward or outward after seeds are shed.
  2. Capsule cylindrical (Fig. 10), rarely enlarged in the upper third or somewhat petiolate, not fused with the subtending bract .... Series *Allochroa* (p. 489)
  2′. Capsule generally gradually narrower upward from a broad base (Fig. 11), evidently fused with the subtending bract for a short distance .. Series *Clelandia* (p. 585)

KEY TO THE SPECIES OF *Oenothera* SECT. *Oenothera* IN SOUTH AMERICA

1. Seeds prismatic Subsect. (*Euoenothera*).
  2. Floral tube 2–5 cm long.
    3. Petals 3.5–5 cm long .... 48. *O. erythrosepala*
    3′. Petals 1–2.5 cm long .... *O. biennis* (p. 618)
  2′. Floral tube 1–1.8 cm long .... 49. *O. villosa* subsp. *strigosa*

1′. Seeds not prismatic.
  4. Buds nodding or the floral tube of the oldest buds curved upward Subsect. (*Raimannia*).
    5. Petals 0.5–1.5 cm long.
      6. Sepals often flecked with red; apices of the sepals 0.5–1 mm long .... 46a. *O. laciniata* subsp. *pubescens*
      6′. Sepals never flecked; apices of the sepals 1–2 mm long .... 46b. *O. laciniata* subsp. *laciniata*
    5′. Petals 2.5–5 cm long .... 47. *O. drummondii*
  4′. Buds not nodding; floral tubes not curved upward Subsect. (*Munzia*).
    7. High mountain plants of very condensed habit, either flowering in the rosette or forming short, prostrate side branches; capsules 1–2 cm long.
      8. Plants forming a rosette only, rarely with short side branches; capsules standing out at right angles from the stem .... 13. *O. nana*
      8′. Plants with prostrate side branches 5–20 cm long; capsule ± appressed to the stem .... 45. *O. punae*
    7′. Plants neither rosette-forming nor prostrate, or taller than 15 cm, erect or prostrate, but if prostrate, then the capsules more than 2 cm long.

9. Capsule urn-shaped, gradually narrowed toward the tip, erect, 4–9 mm thick at the base and with the subtending leaf fused to it; valves of the capsule spreading after seeds are shed; exclusively mountain plants (series *Renneria* in large part).
  10. Floral tube 6–10 cm long; flowers exceeding the apex of the stem in length.
    11. Plants forming a rosette, with a crowded inflorescence; pubescence strigillose and erect villous; petals 2.5–4.5 cm long ...... 5. *O. longituba*
    11′. Plants not forming a rosette, with a more slender and lax inflorescence; pubescence strigillose and appressed villous; petals 2–3 cm long ...... 11. *O. recurva*
  10′. Floral tube 1.2–5.5 cm long; flowers mostly not exceeding the apex of the stem in length.
    12. Floral tube 2.5–5.5 cm long.
      13. Plants with appressed and erect pubescence, sometimes also glandular-pubescent.
        14. Buds narrowly lanceolate to oblong in outline; petals 2–3.5 cm long; seeds mostly flecked with dark spots, 0.8–1.3 mm long; plants glandular pubescent at times ...... 8. *O. scabra*
        14′. Buds lanceolate in outline; petals 1.5–2.5 cm long; seeds almost always immaculate; plants never glandular pubescent ...... 12. *O. sandiana*
      13′. Pubescence all appressed.
        15. Upper bracts with red margins; petals often reddish near the base and along the veins; seeds dark brown to almost black, 1.3–1.5 mm long ...... 10. *O. tarijensis*
        15′. Bracts without red margins; petals entirely yellow; seeds light brown to dark brown, flecked with reddish brown, 0.8–1.2 mm long.
          16. Leaves regularly and acutely serrate; bracts evidently petiolate; seeds 0.8–1 mm long ...... 7. *O. pedunculifolia*
          16′. Leaves irregularly and bluntly serrate; bracts sessile; seeds 1–1.2 mm long ...... 6. *O. tafiensis*
    12′. Floral tube 1.2–2.5 cm long.
      17. Plants with both appressed and erect pubescence.
        18. Plants 1–3.5 dm tall; floral tube 1.5–2 cm long; petals 1.5–2 cm long, reddish at the base and along the veins ... 3. *O. lasiocarpa*
        18′. Plants 5–12 dm tall; floral tube 2–2.5 cm long; petals 2–3 cm long, entirely yellow ...... 4. *O. santarii*
      17′. Plants with appressed pubescence only.
        19. Bracts reddish along the margins; petals red or with a red spot at the base and reddish along the veins ...... 2. *O. versicolor*
        19′. Bracts not reddish; petals entirely yellow.
          20. Plants forming a rosette; petals 1.5–2.5 cm long; capsule 6–9 mm thick ...... 1. *O. peruana*
          20′. Plants not forming a rosette; petals 0.8–1.2 cm long; capsule 4–5 mm thick ...... 9. *O. rubida*
9′. Capsule ± cylindrical, at most tapering toward the apex, erect or standing out from the stem, 1.5–4 mm thick, rarely somewhat thicker, usually only indistinctly fused with the subtending leaf if at all; valves of the capsule spreading or curved inwardly or outwardly when ripe after seeds are shed.
  21. Floral tube 7–11(–13) cm long.
    22. Plants forming a rosette; pubescence thick and shaggy; bracts shorter than the capsule they subtend ...... 17. *O. longiflora*
    22′. Plants not forming a rosette; pubescence soft; bracts longer than the capsule they subtend.
      23. Bracts cultrate to narrowly lanceolate; capsule 2.5–4 cm long, 3–4 mm thick, somewhat enlarged in the upper third; seeds 1.5–2 mm long ...... 20. *O. affinis*
      23′. Bracts lanceolate to narrowly ovate; capsule 2–3 cm long, 4–5

mm thick, not enlarged above; seeds 1.1–1.5 mm long .... 38. *O. elongata*

21′. Floral tube at most 6.5 cm long.

24. Capsule narrowed at the base and at the apex, apparently stipitate; valves of the capsule spreading when seeds are shed; annual plants, mostly less than 3 dm tall.

25. Plants mostly unbranched; leaves remotely and bluntly serrate; floral tube 0.6–1.1 cm long; seeds 1.5–1.7 mm long, dark brown to almost black .... 29. *O. verrucosa*

25′. Plants branched; leaves sinuate-toothed; floral tube 1–3 cm long; seeds 1–1.3 mm long, brown .... 31. *O. arequipensis*

24′. Capsule not narrowed at the base; valves curving when seeds are shed.

26. Leaves with long, narrow teeth, these often secondarily toothed, or leaves remotely and bluntly serrate; valves of the capsule curving inward when seeds are shed; seeds narrowly elliptic in outline, 1.2–1.6 mm long, 0.4–0.5 mm thick .... 30. *O. coquimbensis*

26′. Leaves without long, narrow teeth; valves of the capsule curving outward or spreading when seeds are shed; seeds elliptic to broadly elliptic in outline.

27. Plants with exclusively appressed pubescence.

28. Petals 2.5–4.5 cm long .... 33. *O. featherstonei*

28′. Petals less than 2.5 cm long.

29. Bracts linear .... 14. *O. mendocinensis*

29′. Bracts not linear.

30. Capsule 3–4.5 cm long, 3–4 mm thick .... 24. *O. bahia-blancae*

30′. Capsule less than 3 cm long, 2–3.5 mm thick.

31. Capsule shorter than the subtending bract .... 28b. *O. parodiana* subsp. *strigulosa*

31′. Capsule longer than the subtending bract.

32. Bracts lanceolate to ovate, truncate to subcordate at the base; leaves with blunt teeth; seeds elliptic in outline, 1.3–1.5 mm long 0.5–0.7 mm thick .... 32. *O. grisea*

32′. Bracts narrowly elliptic to lanceolate, attenuate at the base; leaves mostly sinuate-toothed; seeds broadly elliptic in outline, 1.3–1.8 mm long, 0.8–0.9 mm thick .... 34. *O. nocturna*

27′. Plants with some erect pubescence.

33. Bracts linear .... 14. *O. mendocinensis*

33′. Bracts not linear.

34. Petals 2.5–5 cm long.

35. Bracts narrowly oblong to lanceolate, rounded at the base; plants not forming a rosette .... 18. *O. catharinensis*

35′. Bracts lanceolate to narrowly ovate, truncate to subcordate at the base; plants forming a rosette.

36. Bracts longer than the capsule they subtend .... 15. *O. odorata*

36′. Bracts shorter than the capsule they subtend, or at most subequal to it.

37. Bracts usually only half as long as the capsule they subtend, or even shorter; floral tube (3–)3.5–5.5 cm long; capsule 2.5–3.5 cm long; seeds 1.3–1.5 mm long .... 16a. *O. ravenii* subsp. *ravenii*

37′. Bracts more than half as long as the capsule they subtend; floral tube 2.5–3.5 cm

long; capsule 3.5–5 cm long; seeds 1.5–1.8 mm long .... 23b. *O. stricta* subsp. *altissima*

34′. Petals at most 2.5 cm long.
38. Capsule 1–1.5 cm long .... 42. *O. brevipetala*
38′. Capsule longer.
39. Capsule 1.5–2.5 mm thick.
40. Plants exclusively short-villous and glandular-pubescent, appearing glabrous when viewed without a lens .... 19b. *O. indecora* subsp. *bonariensis*
40′. Plants with erect, long villous pubescence in part.
41. Capsule 3.5–6 cm long .... 22. *O. rivadaviae*
41′. Capsule at most 3 cm long.
42. Bracts only half as long as the capsule they subtend or shorter, truncate to subcordate at the base .... 28a. *O. parodiana* subsp. *parodiana*
42′. Bracts subequal to or longer than the capsule they subtend.
43. Plants strigulose, villous, and glandular-pubescent; bracts evidently longer than the capsule they subtend .... 44. *O. tucumanensis*
43′. Plants only villous and glandular-pubescent; bracts subequal to or shorter than the capsule they subtend.
44. Plants forming a rosette, ± villous; sepals often flecked with dark red; capsule 1.5–2 mm thick; seeds 1–1.3 mm long .... 19a. *O. indecora* subsp. *indecora*
44′. Plants not forming a rosette, densely villous; sepals not flecked with red; capsule 2–2.5 mm thick; seeds 1.5–1.6 mm long .... 26. *O. montevidensis*
39′. Capsule 3–4 mm thick.
45. Bracts longer than the capsule they subtend.
46. Plants only villous and glandular-pubescent; capsule standing out obliquely from the stem.
47. Plants very densely long-villous.
48. Bracts rounded to truncate at the base, those towards the tip of the stem erect and somewhat imbricate .... 21. *O. mollissima*
48′. Bracts truncate to subcordate at the base, spreading .... 25. *O. picensis*
47′. Plants not very densely long-villous .... 25. *O. picensis*
46′. Plants strigillose and villous; in part also glandular-pubescent; capsule ± erect.
49. Plants densely long-villous; petals 0.8–1.3 cm long .... 39. *O. pseudoelongata*
49′. Plants with various pubescence; petals at least 1.5 cm long.
50. Plants forming a rosette; floral

tube 1.3–2.5(–3) cm long; seeds immaculate.

51. Bracts evidently longer than the capsule they subtend, without red margins; capsule 2.5–4 cm long; seeds 1.4–2 mm long ...... 35. *O. magellanica*

51′. Bracts slightly longer than to shorter than the capsule they subtend, with red margins; capsule 2–3 cm long; seeds 1.1–1.5 mm long .. 36. *O. villaricae*

50′. Plants not forming a rosette; floral tube 3–6 mm long; seeds flecked with reddish brown.

52. Bracts only a little longer than the capsule they subtend or shorter, mostly with red margins .... 41. *O. siambonensis*

52′. Bracts evidently longer than the capsule they subtend, without red margins .... 43. *O. acuticarpa*

45′. Bracts subequal to or shorter than the capsule they subtend.

53. Capsule suberect.

54. Plants forming a rosette; seeds immaculate.

55. Floral tube 2–3 cm long .... 36. *O. villaricae*

55′. Floral tube 4–4.5 cm long .... 37. *O. hechtii*

54′. Plants not forming a rosette; seeds flecked with reddish brown.

56. Floral tube 1.5–2.5 cm long; capsules with the 4 valves evidently free and crenate at the apex .... 40. *O. cordobensis*

56′. Floral tube 3–5.5 cm long; capsule without evidently free valves .... 41. *O. siambonensis*

53′. Capsule standing out from the stem.

57. Petals at most 1.5 cm long.

58. Plants not forming a rosette; floral tube 3–4.5 cm long .... 25b. *O. picensis* subsp. *cordobensis*

58′. Plants forming a rosette; floral tube at most 3 cm long.

59. Capsule 3–4.5 cm long .... 24. *O. bahia-blancae*

59′. Capsule 2.5–3 cm long.

60. Floral tube 1.8–3 cm long; buds 10–17 mm long; petals 1.2–2 cm long .... 16b. *O. ravenii* subsp. *argentinae*

60′. Floral tube 1–2 cm long; buds 5–8 mm long; petals 0.7–1.2 cm long .... 28a. *O. parodiana* subsp. *parodiana*

57′. Petals more than 1.5 cm long.
61. Floral tube more than 4 cm long.
62. Floral tube usually more than 4.5 (–6.5) cm long; buds narrowly oblong to oblong in outline .. 27. *O. pseudolongiflora*
62′. Floral tube at most 4.5 cm long; buds lanceolate in outline.
63. Upper bracts with arched incurved apices; plants with long, bristly hairs, especially below .... 28c. *O. parodiana* subsp. *brasiliensis*
63′. Upper bracts plane; plants strigillose, especially below, never with long, bristly hairs .. 23a. *O. stricta* subsp. *stricta*
61′. Floral tube less than 4 cm long.
64. Bracts at most half the length of the capsule they subtend .... 16. *O. ravenii*
64′. Bracts more than half the length of the capsule they subtend.
65. Upper bracts erect .... 23c. *O. stricta* subsp. *argentinae*
65′. Upper bracts spreading.
66. Rosette leaves 0.8–1.3 cm wide; cauline leaves 0.6–1 cm wide; bracts 0.7–1.2 cm wide; seeds 1.5–1.8 mm long .... 23a. *O. stricta* subsp. *stricta*
66′. Rosette leaves 1.2–3 cm wide; cauline leaves 1–2.5 cm wide; bracts 1.2–2 cm wide; seeds 1.2–1.5 mm long .. 28c. *O. parodiana* subsp. *brasiliensis*

Series I. RENNERIA

Oenothera sect. **Oenothera** subsect. **Munzia** series **Renneria** (Fischer) Dietrich, stat. nov. Based on *Oenothera* subgen. *Renneria* Fischer, Feddes Repert. Spec. Nov. Regni Veg. 64: 233. 1962

Onagra sensu Krause, Repert. Spec. Nov. Regni Veg. 1: 167. 1905.

Oenothera § *Euoenothera* sensu Munz & Johnston, Contr. Gray Herb. 75: 17. 1925, pro parte.

Oenothera subgen. *Euoenothera* sensu Munz, Physis 11: 280. 1933; Revista Univ. (Santiago) 22: 262. 1937, pro parte; sensu Hagen, Indiana Univ. Publ. Sci. Ser. 16: 306. 1950, pro parte.

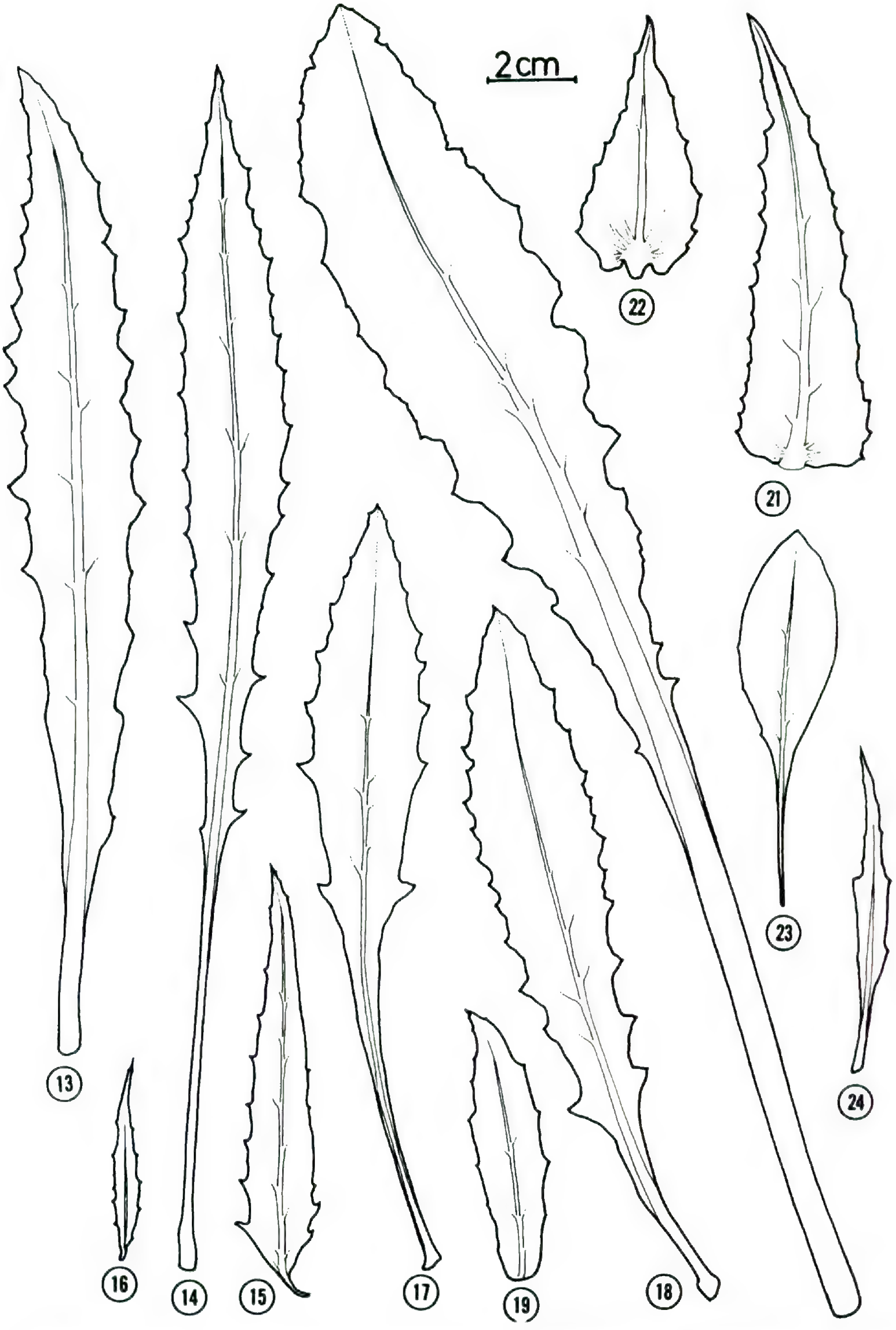
Oenothera subgen. *Raimannia* Munz, Physis 11: 279. 1933, pro parte; Amer. J. Bot. 22: 645. 1935, pro parte.

Erect annual or biennial, possibly sometimes perennial, herbs, forming a rosette or elongating soon after germination, sometimes flowering in the rosette, simple or with a ± branched main stem and arcuate to oblique side branches arising from the rosette; plants less than 1 dm to 15 dm tall. Plants very densely to sparsely strigillose, often also appressed or erect long-villous, rarely glandular-pubescent. Rosette leaves linear to lanceolate, acute, narrowed gradually or ± abruptly to the petiole, rarely sessile, 2.5–35 cm long, 0.3–6 cm wide; cauline leaves linear, elliptic or lanceolate, acute, sessile and acute to truncate at the base, or narrowly cuneate at the base and with a long or short petiole, 3–20 cm long, 0.3–3 cm wide; bracts linear, elliptic or lanceolate, acute, sessile and acute to subcordate at the base or attenuate at the base and with a long or short petiole, 3–12 cm long, 0.3–2.5 cm wide, longer than the capsules they subtend; leaves ± regularly or irregularly serrate, plane or undulate at the margins, sometimes (in *O. nana*) flecked with black. Inflorescence simple or branched, mostly crowded; flowers mostly obliquely erect, (1–)2–6 opening toward the apex each day. Floral tube 0.5–10 cm long, usually curved. Buds oblong to narrowly ovate in outline, 0.4–3.5 cm long, 3–8 mm thick, often with red stripes at the junction of the sepals with the floral tube, and sometimes also along the midveins. Sepals green, yellowish, or yellowish green, often flushed with red; apices of the sepals 1–4 mm long, erect or divergent. Petals very broadly obovate, rounded or retuse, 0.5–4 cm long, yellow or bright yellow, sometimes flushed with red along the veins and at the base, or completely red. Ovary 0.8–1 cm long. Capsule oblong or lanceolate to ovate in outline, 1–3 cm long, 3–10 mm thick, erect and ± appressed to the stem, or (in *O. nana*) standing out at right angles from the prostrate stems, evidently fused with the bracts; valves spreading apart in dehiscence or slightly incurved at the apex only. Seeds ± obtusely angular, rounded and elliptic in outline, 0.8–1.7 mm long, 0.5–1 mm thick, light brown to dark brown or black, sometimes with darker flecks. Self-compatible; outcrossing or self-pollinating chromosomal homozygotes or self-pollinating complex heterozygotes. Gametic chromosome number, $n = 7$ (bivalents, ring of 14, or intermediate configurations at meiotic metaphase I).

Lectotype species: *Oenothera versicolor* Lehm: = *O. campylocalyx* Koch & Bouché.

Distribution (Fig. 7): All species of this subsection are exclusively mountain plants and occur at elevations from 1,500 to 5,000 m, rarely lower. They occur at these elevations in the Cordillera Occidental and Cordillera Oriental of Peru from the province of Lambeyeque southward a short distance over the Chilean border. In the Bolivian and Argentine Andes, the group ranges along the eastern flanks southward to Mendoza. Disjunct stations occur in the Sierra of Córdoba and in the Andes of Ecuador near Quito, the latter probably resulting from the naturalization of cultivated plants.

The characteristic aspect of the plants of this section results from their thick stems, sometimes up to 2 cm in diameter, crowded inflorescences, and obliquely ascending flowers with somewhat curved floral tubes. Most diagnostic, however, are the erect, urn-shaped or broadly cylindrical capsules (Fig. 9). The



FIGURES 13–24. Leaves of South American taxa of *Oenothera* sect. *Oenothera*.—13. Rosette leaf of *O. peruana* (Peru, Arequipa, *Santarius 2090*).—14–16. Rosette leaf, cauline leaf, and bract of *O. versicolor* (Bolivia, Cochabamba, *Diers in 1959*).—17–19. Rosette leaf, cauline leaf, and bract of *O. tafiensis* subsp. *tafiensis* (Argentina, Tucumán, *Santarius 1733*).—

three first species are annual, although potentially overwintering as a rosette and therefore biennial, whereas *O. santarii* and *O. longituba* are obligate biennials in nature, although flowering the first year in cultivation. These five species have somewhat angular seeds which are dark brown or black.

Oenothera scabra forms only a few leaves near the base on germination, and then grows into a branching plant without forming a rosette. Its seeds are rounded in outline, smaller than those of the first-listed and presumably more generalized species of the series, light brown, and flecked. *Oenothera tafiensis* and *O. pedunculifolia* can be considered intermediate between *O. scabra* and the remaining species; thus *O. tafiensis* subsp. *tafiensis* resembles *O. peruana* in habit, but has small flecked seeds. In *O. tafiensis* subsp. *parviflora* and *O. pedunculifolia*, both also with flecked seeds, the plants bolt from a rosette of limited size and resemble *O. scabra* in habit.

1. **Oenothera peruana** Dietrich, sp. nov.—Figs. 13, 102, 168.

Herba annua vel biennis, erecta, rosulata, 5–10 dm alta, simplex vel caulis principalis ramosus et ramis oblique e rosula ascendentibus. Herba tota dense strigulosa, circum inflorescentiam pilis longis adpressis praedita. Folia rosulae angustissime elliptica vel anguste oblanceolata, acuta, lamina in petiolum brevem gradatim decrescens, 15–20 cm longa, 2–5 cm lata; folia caulina linearia vel cultrata ad anguste lanceolata, acuta, basi acuta, 6–20 cm longa, 1–3 cm lata, breviter petiolata; bractea linearia vel anguste obovata, acuta, basi truncata, sessilia, 3–6 cm longa, 0.8–2 cm lata; folia omnia irregulariter ± serrata. Inflorescentia simplex. Tubus floralis 1.2–2 cm longus. Gemmae ambito lanceolatae, 1.5–2.5 cm longae, 5–7 mm crassae, griseovirides vel flavovirides; apices sepalorum ca. 2 mm longi, erecti. Petala latissime obovata, floride lutea, post anthesem decolorata, 1.5–2.5 cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato. Ovarium 7–10 mm longum. Capsula 2–3 cm longa, 6–9 mm crassa, maturitate brunnea. Semina obtuse angulata, 1.2–1.7 mm longa, 1–1.2 mm crassa, nigra. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice admodem homozygotica.

Erect annual or biennial herb, forming a rosette, 5–10 dm tall. Main stem simple or somewhat branched, with side branches arising obliquely from the rosette. Entire plant densely strigillose, in the region of the inflorescence also with appressed long-villous pubescence. Rosette leaves very narrowly elliptic to narrowly oblanceolate, acute, gradually narrowed to the petiole, 15–20 cm long, 2–5 cm wide; cauline leaves linear or cultrate to narrowly lanceolate, acute, acute at the base, 6–20 cm long, 1–3 cm wide, with a short petiole; bracts linear to narrowly obovate, acute, truncate at the base, sessile, 3–6 cm long, 0.8–2 cm wide; all leaves irregularly and ± prominently serrate, plane or undulate at the margins. Inflorescence unbranched. Floral tube 1.2–2 cm long. Buds lanceolate in outline, 1.5–2.5 cm long, 5–7 mm thick, gray green or yellowish green; apices of sepals erect, ca. 2 mm long. Petals very broadly obovate, bright yellow, fading after anthesis, 1.5–2.5 cm long. Anthers 6–9 mm long. Filaments 8–11 mm long. Style long, the style held above the anthers at anthesis, 2–4.5 cm long. Stigma lobes 4–7 mm long. Ovary 7–10 mm long. Capsule 2–3 cm long,

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20–22. Rosette leaf, cauline leaf, and bract of *O. santarii* (Argentina, Mendoza, *Santarius 1430*).—23. Rosette leaf of *O. tafiensis* subsp. *parviflora* (Argentina, Tucumán, *Göpel in 1961*).—24. Rosette leaf of *O. nana* (Peru, Puno, *Santarius 2045*).

6–9 mm thick, dark brown to very dark brown when ripe. Seeds 1.2–1.7 mm long, 1–1.2 mm thick, obtusely angular, black. Self-compatible but outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 8 and 3 bivalents **, ring of 12 and 1 bivalent ***, or ring of 14**** at meiotic metaphase I). Flowering time: December–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 25 July 1972. Source: Peru, Dep. Arequipa, moist slope and edge of an irrigation ditch 19 km behind Arequipa at road to Chihuata/Puno, 2,700 m, 13 Apr. 1968, *K. A. Santarius 2090* (MO-2155406, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 225): Very local in the Andes of south Peru and north Chile, 2,500–3,300 m elevation.

Specimens examined from cultivated plants:

PERU. AREQUIPA: Ca. 19 km behind Arequipa at the road to Chihuata/Puno, 2,700 m, *Santarius 2075, 2088***, 2090*, 2091*, 2096***, 2098*, 2102*, 2103*, 2104***, 2106*, 2107**, **, *2108***** (DUSS, *2098* also CTES, *2075, 2088, 2090, 2096, 2098, 2106, 2108* also MO; *2090, 2098, 2106* also M).

Additional specimens examined:

PERU. APURIMAC: Abancay, 3,100 m, *Iltis & Ugent 695* (UC). AREQUIPA: Chihuata, 20 km E of Arequipa, *Munz 15539* (POM). Pichu-Pichu, 3,300 m, *Sandemann 3778* (K). Cailloma, 3,180 m, *Lopez 284* (RSA).

CHILE. TARAPACÁ: Mamiña, *Pfister 9451* (CONC).

In contrast to all of the following species, *O. peruana* has clearly angled seeds. On the basis of this characteristic, it seems to stand closest to the common origin of the South American species of sect. *Oenothera* with the North American ones that have been called subgen. *Euoenothera*.

It is possible that complex heterozygotes arise from time to time in the zone of overlap between *O. peruana* and *O. versicolor*, since some plants with a ring of 14 (*Santarius 2108*) are intermediate between these species. These plants are morphologically indistinguishable from *O. peruana*, and are not taken as representing an independent species. Plants with smaller rings of chromosomes are regarded as hybrids between chromosomally structurally differentiated individuals of *O. peruana*.

2. **Oenothera versicolor** Lehm., Ind. Sem. Hort. Bot. Hamb. 7. Dec. 1855; Linnaea 28: 359. 1856.—FIGS. 14–16, 103–104, 169.

O. campylocalyx Koch & Bouché, Ind. Sem. Hort. Berol. App. 17. 1856. LECTOTYPE: Cultivated in Berlin Botanical Garden, 1832, ex herb. Kunth, source unknown (B, destroyed; POM, fragments and photographs).

O. coccinea Britton, Bull. Torrey Bot. Club 17: 213. 1890. LECTOTYPE: Bolivia, Dep. Potosí, Ingenio del Oro, 3,280 m, Mar. 1886, *H. H. Rusby 1815* (NY); Munz & Johnston, Contr. Gray Herb. 75: 22. 1925.

Onagra fusca Krause, Repert. Spec. Nov. Regni Veg. 1: 167. 1905. TYPE: Peru, Dep. Ancash, near Pampa Romas, between Samanco and Caraz, among herbs, especially grasses and shrubs, 3,200–3,500 m, *A. Weberbauer 3211* (B, destroyed in World War II, POM, photograph).

Oenothera campylocalyx sensu Macbride, Field Mus. Nat. Hist., Bot. Ser., 13(4): 535. 1941, pro parte.

O. rubida sensu Macbride, Field Mus. Nat. Hist., Bot. Ser., 13(4): 540. 1941, pro parte.

O. kopenhagensis Latzel, Biol. Zentralbl. 86. 409. 1967. Invalid name. = *Oenothera versicolor* Lehm.

O. campylocalyx sensu Munz, Opera Bot., Ser. B, 3: 39. 1974, pro parte.

Erect annual or biennial herb, forming a rosette, 5–8 dm tall. Plants unbranched or with a scarcely branched main stem and with arcuate-ascending side branches from the rosette. Lower portion of plants sparsely strigillose, becoming densely so in the region of the inflorescence, where also with an admixture of appressed and erect long-villous pubescence. Rosette leaves narrowly lanceolate, acute, gradually narrowed to the petiole, 20–25 cm long, 1.5–3.5 cm wide; cauline leaves very narrowly elliptic to narrowly lanceolate, acute, narrowly cuneate at the base, 8–12 cm long, 0.6–2 cm wide, sessile or with a short petiole; bracts linear to very narrowly elliptic or narrowly lanceolate, acute, acute to truncate at the base, 5–10 cm long, 0.5–2 cm wide; leaves plane or undulate at the margins, ± regularly serrate with acute or rounded teeth, the margins reddish, especially in the bracts of the young buds. Inflorescence mostly unbranched. Floral tube 1.2–2.5 cm long. Buds lanceolate in outline, 1.5–2 cm long, 5–7 mm thick when mature, reddish at the junction of the sepals with the floral tube; apices of the sepals erect or divergent, 2–3 mm long. Petals very broadly obovate, rounded or retuse, 1.2–2 cm long, yellow, red near the base and along the veins or entirely red. Anthers 5–8 mm long. Filaments 6–10 mm long. Style mostly short, the anthers shedding pollen directly on the stigma at anthesis, but sometimes longer, the stigma elevated above the anthers, 2–3.5 cm long. Stigma lobes 2.5–4.5 mm long. Ovary 8–10 mm long. Capsule 1.5–3 cm long, 5–9 mm thick, glabrescent, dark brown to very dark brown when ripe. Seeds 1–1.3 mm long, 0.6–0.7 mm thick, ± obscurely angled, dark brown to black. Self-compatible; self-pollinating or outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: Ecuador and Peru, December–June; Bolivia, October–May; Argentina, October–April.

Type: not seen. The original description clearly indicates the species described here.

Distribution (Fig. 226): Andes of Peru, Bolivia, and Argentina from the department of Ancash in Peru through Bolivia to the province of La Rioja in Argentina, 2,000–4,500 m elevation. The occurrence in Ecuador (Pinchincha Prov.) might represent the establishment of adventive plants.

Specimens examined from cultivated plants:

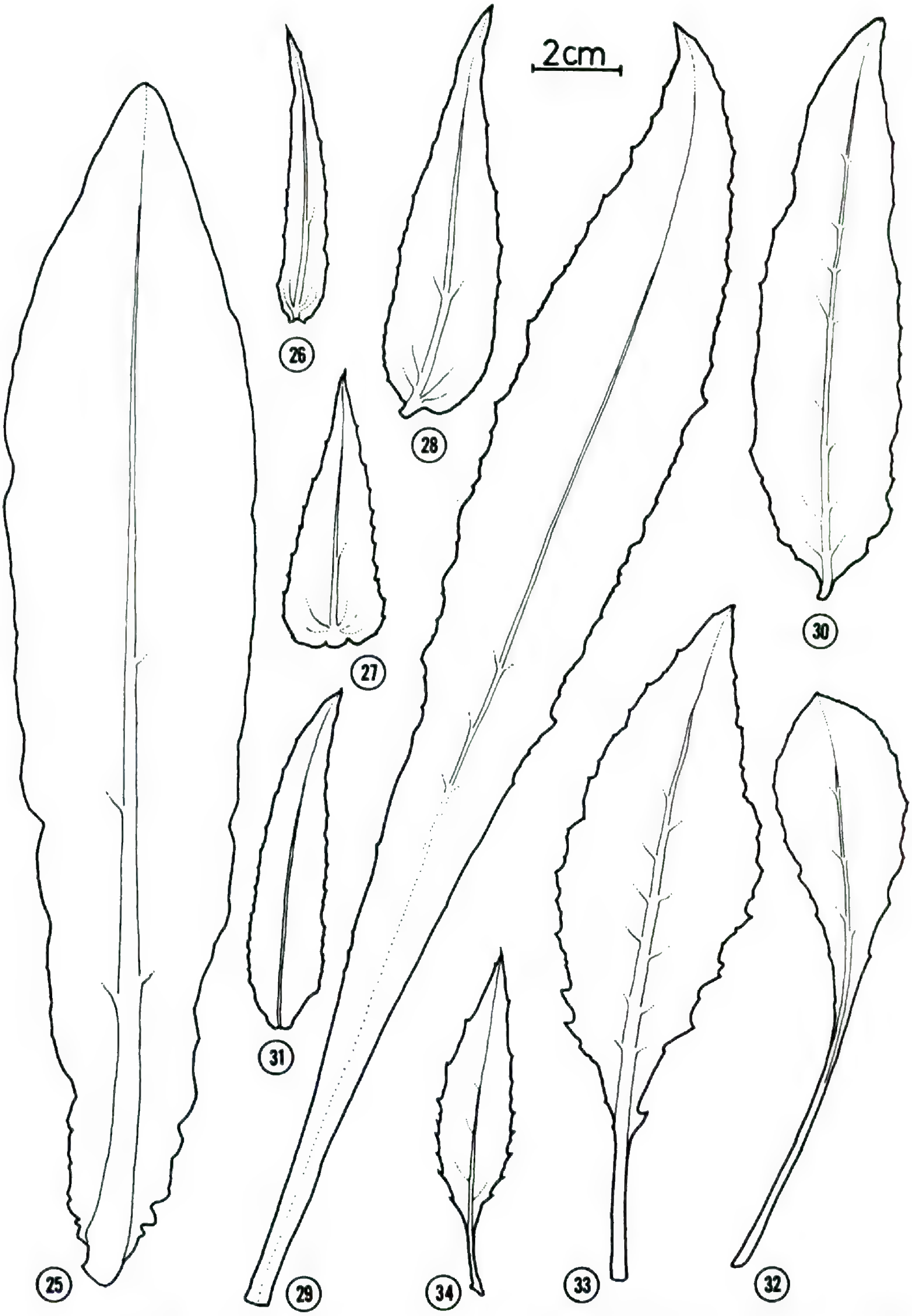
PERU. JUNÍN: Valley of Río Mantaro, Pachacayo, 3,650 m, *Santarius 2163**, *2180*, *2184* (DUSS, MO; *2163* also CTES, M). PUNO: Chimu, 8 km SE of Puno, *Santarius 2062** (DUSS).

BOLIVIA. COCHABAMBA: Liriuni near Cochabamba, *Diers in April 1959** (CTES, DUSS, MO). TARIJA: Road from Tarija to Villazón, km 33, 3,100 m, *Santarius 1946** (CTES, DUSS, M, MO).

Additional specimens examined:

ECUADOR. PINCHINCHA: Between Nono and Cotocollao, 3,100 m, *Asplund 20276* (LD, NY, R, S, UPS). W of Nono, 2,700 m, *Harling et al. 10253* (RSA).

PERU. ANCASH: Huaylas, Laguna Parón, 3,000 m, *Lopez 1878* (RSA). HUÁNUCO: Huacachi, near Muña, *Macbride 3884* (F, G, GH, US). Pillao, 2,700 m, *Woytowski in 1946* (F, MO, LIL, UC). LIMA: Río Blanco, 3,900 m, *Macbride & Featherstone 681* (F, GH). Rimac valley, 3,500 m, *N.N. in 1954* (RSA). Chicla near Huarochiri, 4,000 m, *Saunders 594* (BM). Oroya near Lima, *Kalenborn 41* (MO), *241* (GH, NY, US). AYACUCHO: Pampa de Chupas, *N.N. in 1969* (RSA). APURIMAC: Apurimac River near Cañas, 3,700 m, *Vargas 11044* (F, GH, K, UC). CUZCO: Cuzco, *Herrera in 1922* (SI); 3,350 m, *Balfour 102* (K). Paucartambo, Huaisampillo, 2,200 m, *Vargas 9976* (MO). Ollantaytambo, 3,000 m, *Cook & Gilbert 628* (US). PUNO: Puno, 4,000 m, *Soukup 109* (F). Carabaya, Antapampa, 4,180 m, *Vargas*



FIGURES 25–34. Leaves of South American taxa of *Oenothera* sect. *Oenothera* (continued).—25. Rosette leaf of *O. longituba* (Argentina, Catamarca, *Diers in 1959*).—26. Bract of *O. tarijensis* (Bolivia, Tarija, *Santarius 1924*).—27. Bract of *O. recurva* (Bolivia, Tarija, *Santarius 1941*).—28. Bract of *O. scabra* (Bolivia, Cochabamba, *Santarius 2003*).—29–31. Rosette leaf, cauline leaf, and bract of *O. longituba* (Argentina, Jujuy, *Fabris 5787*).—32–34. Rosette leaf, cauline leaf, and bract of *O. pedunculifolia* (Argentina, Tucumán, *Santarius 1745*).

7002 pro parte (LIL, POM). Azángaro, Tequena near Arapa, 3,900 m, *Aguilar 227* (USM). Capachica Peninsula of Titicaca Lake, 3,700 m, *Tutin 1009* (BM).

BOLIVIA. LA PAZ: La Paz, 3,800 m, *Buchtien 532* (GH, NY, UC, US). Tacacoma, *Cárdenas 5137* (US). Charasani near Muñecas, 2,700 m, *Cardenas 3844* (POM). Quime, 2,400 m, *Brooke 5396* (BM). Isla Titicaca, 3,840 m, *Buchtien 2921* (NY, US). Pongo, 3,650 m, *Tate 190* (NY). Titicaca, *Adolph & Bandelier in 1905* (NY). Vicinity of Sorata near Larecaja, 3,200 m, *Mandon 628* (P pro parte, S), *627* (BM, G, K, P, W pro parte). Gran Poder near Sorata, 3,050 m, *Brooke 6644* (BM). COCHABAMBA: 30 mi ENE Cochabamba, 3,750 m, *Brooke 5091* (BM). Choro above the Cocapata River, 3,050 m, *Brooke 6028* (BM, F, NY). ORURO: Caranga, *D'Orbigny in 1929* (P). POTOSÍ: Ingenio de Oro, 3,050 m, *Rusby 1976* (NY). CHUQUISACA: Cordillera de Sombreros, 3,100 m, *Troll 670* (M). TARIJA: La Aguada near Tarija, 3,300 m, *Balls 6112* (K, UC, US).

ARGENTINA. JUJUY: Chorru Valley near Tilcara, 3,400 m, *Balls 6027* (K). Tilcara, Falda Grande, Cerro de Guairahuasi, 3,400 m, *Cabrera & Hernandez 14021* (LP). Sierra de Zenta, 4,000–4,500 m, *Budín 178* (GH, POM). Tumbaya, *Medinacely 9* (POM). Cerro Morado near Tumbaya, 3,300 m, *Fabris 6217* (BAA); *Cabrera 18306* (LP). Volcán near Tumbaya, 2,900 m, *Sleumer 3563* (LIL). Serrania de Calilegua, Tolditos, 2,600 m, *Fabris et al.* (LP). Serrania de Calilegua, Cerro Colorado, 2,700 m, *Fabris et al.* (LIL, LP). Purmamarca, Tascal near Tumbaya, 3,400 m, *Cabrera 15105* (LP). Puente del Diablo near Tres Cruces, 4,000 m, *Fabris & Marchionni 1746* (LP). Mina Aguilar near Tumahuaca, *Fernández 2003* (LP). Mina Aguilar, 4,400 m, *Sleumer 3383* (LIL). Mula Muerte, 2,700 m, *Castillón 119, 130* (LIL). SALTA: El Alisal near Cafayate, 2,800 m, *in 1914* (LIL). Santa Victoria, 2,385 m, *Sleumer 3780* (LIL). Lizoite near Sta. Victoria, 3,340 m, *Meyer & Bianchi in 1940* (LIL). TUCUMÁN: La Ciénaga, *Lorentz & Hieronymus 687, 689* (CORD, GOET); *Lillo 3707* (LIL). Cerro Negrito near Tafí, 3,500–3,600 m, *Sparre 6147* (LIL). La Queñua of the Sierra Calchaquies, 3,000 m, *Burkart 5366* (SI). Estancia Sta. Boza and Pto. La Cueva, 3,600 m, *Venturi 3165* (LIL, US). Malamala, 2,400 m, *Lillo 3443* (LIL). El Chorro near Trancas, 2,500–3,000 m, *Schreiter 1121* (LIL). CATAMARCA: Andalgala, *Jorgensen 1054* pro parte (LIL). LA RIOJA: Sierra de Famatima, slope of La Mesada, 3,500–3,700 m, *Kurtz 13946* (CORD). Between La Mesada and El Paso, 3,500–4,200 m, *Kurtz 14040* (CORD).

Early specimens from cultivated plants:

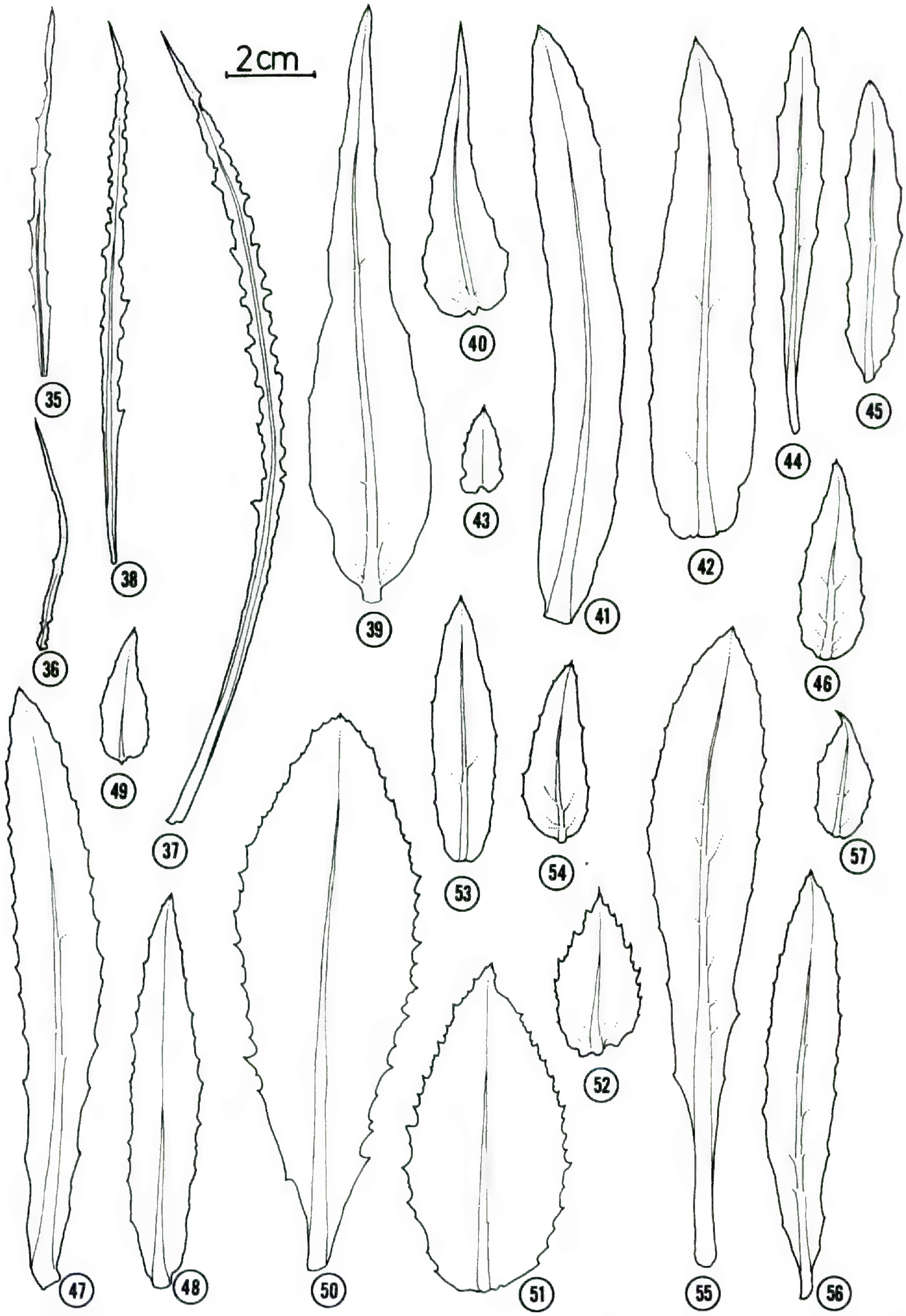
Ex herb. *J. Gay*, Jardin Vilmorin, Paris, 17 Aug. 1859, (K; as *O. versicolor*). Hort. Paris, Aug. 1865, *B. Verloti* (P; as *O. campylocarpa*).

The partial or pronounced red coloration of the veins and base of the petals and the predominantly strigillose pubescence are characteristic of *O. versicolor*. As might be expected from the very extensive range, there is a considerable and significant amount of variation, especially in the width of the leaves and their toothing. Plants intermediate with *O. lasiocarpa* occur in the provinces of Tucumán and Jujuy in Argentina. It is not known whether these are spontaneous hybrids or complex heterozygotes which characterize entire populations.

3. **Oenothera lasiocarpa** Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 143. 1874.—FIGS. 105, 170.

O. campylocalyx sensu Munz, Physis 11: 286. 1933, pro parte.

Erect annual or biennial herb, forming a rosette, 1–3.5 dm tall. Plants unbranched or with a somewhat branched main stem and widely arcuate-ascending side branches arising from the rosette. Entire plant densely strigillose, especially in the region of the inflorescence, and also with erect long-villous pubescence. Rosette leaves narrowly oblanceolate to very narrowly elliptic, acute, gradually narrowed to the petiole, 6–12 cm long, 0.8–1.5 cm wide; cauline leaves mostly absent, since the plants generally bloom just above the rosette, but when present very narrowly elliptic, 5–10 cm long, with a short petiole or sessile; bracts narrowly lanceolate to oblanceolate, 3–8 cm long, 0.3–1.2 cm



FIGURES 35–57. Leaves of South American taxa of *Oenothera* sect. *Oenothera* (continued).—35–36. Cauline leaf and bract of *O. mendocinensis* (Argentina, Buenos Aires, *Santarius 421*).—37–38. Rosette leaf and cauline leaf of *O. odorata* (Argentina, Chubut, *Santarius 953*).—39–40. Cauline leaf and bract of *O. odorata* (Argentina, Río Negro, *Santarius 800*).—41–43. Rosette leaf, cauline leaf, and bract of *O. ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul,

wide, acute, acute to truncate at the base; leaves plane or undulate at the margins, irregularly serrate with coarse to slightly produced teeth. Inflorescence unbranched. Floral tube 1.5–2(–2.5) cm long. Buds oblong to narrowly ovate in outline, 1–2 cm long, 6–8 mm thick, often flushed with red; apices of the sepals erect, ca. 2 mm long. Petals very broadly obovate, 1.5–2 cm long, rounded or retuse, red near the base and along the veins. Anthers 4–6 mm long. Filaments 6–8 mm long. Style short, the stigma surrounded by the anthers at anthesis, or long, the stigma held above the anthers at anthesis, 2–3 cm long. Stigma lobes 3–5 mm long. Ovary 8–10 mm long. Capsule 1–2(–2.5) cm long, 5–8 mm thick, dark brown to very dark brown when ripe. Seeds 1–1.2 mm long, 0.6–0.8 mm thick, ± obscurely angled, dark brown. Self-compatible; self-pollinating or outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: November–April.

Type: Argentina, Prov. Catamarca, alpine meadows, Vayas Altas, Sierra de Belén, 2,950–3,650 m, mid-January 1872, *T. G. Lorentz 633* (GOET, holotype; CORD, isotype).

Distribution (Fig. 225): Andes of Argentina, in the provinces of Salta, Jujuy, Tucumán, Catamarca, La Rioja, and San Juan; 2,000–4,000 m elevation.

Specimens examined from cultivated plants:
ARGENTINA. TUCUMÁN: Tafi del Valle, 3,900 m, *Diers in 1959** (CTES, DUSS, M, MO).
Additional specimens examined:
ARGENTINA: JUJUY: Quebrada near Susques, *Cabrera 8760* (LP). Sierra de Zenta, 4,500 m, *Budin 7476* (LIL). Yavi Chico, 3,350 m, *Werner 286* (LP). Maimara, 2,230 m, *Budin 11790* (GH, LIL, POM, SI). Volcán, Loma del Tambo, 2,500–3,000 m, *Schreiter in 1924* (LIL). SALTA: Vicinity of Nevado del Castillo, *Lorentz & Hieronymus 47* (CORD, GOET). TUCUMÁN: Tafi, Cerro Muñoz, 3,000 m, *Lillo 7428, 4267* (LIL); *Castillon 177* (LIL). Río Blanco, 2,600 m, *Lillo 8868* (LIL). Lara near Tafi, 3,200 m, *Rodriguez 574* (GH). Quebrada del Barón, *Fabris 1371* (LP). Quebrada de la Hoyada, 1,500 m, *Schreiter 1875* (LIL). Calchaquies, 4,200 m, *Lillo 5516* (LIL); *Türpe in 1959* (LIL); *La Sota 2791* (LP). Peñas Azules, *Parodi 10971* (POM); *Burkart 5300* (SI); *Olea 8759* (LIL). La Queñoa, 2,800 m, *Schreiter 6995* (LIL). La Ciénaga, 2,800 m, *Sleumer 203* (LIL). Pojonal, 2,600 m, *Meyer & Vaca 23659* (LIL). Casa de Piedra, *Lillo 179* (LIL). Vicinity of Muñecas, *Castillon in 1905* (LIL). Chicligasta, Estancia Las Pavas, 3,000 m, *Venturi 4597* (BAB, LIL, SI). Trancas, Chorro, 3,400 m, *Venturi 8512* (US); *Schreiter 4790* (LIL). CATAMARCA: Andalgala, valley of Río Bolsón, 4,000 m, *Rohmeder in 1943* (LIL). Campo Grande, *Schickendantz 67* (CORD, GOET, SI); *Schickendantz 310* (CORD, GOET). Sierra de Ambato, between El Rodeo and Cerro Manchado, 2,900 m, *Hunziker 19196, 20998* (CORD); *Hunziker & Di Fulvio 19759, 19721* (CORD). Belén, slopes N of Portezuelo, 3,200–3,300 m, *Sleumer & Vervoorst 2606* (LIL, US). Tinogasta, La Tranca, *Castellanos 564* (POM). La Puntilla near Tinogasta, 2,700 m, *Hunziker 4356* (BAB). LA RIOJA: Sierra Famatina, La Vega de la Mesada, 3,650 m, *Kurtz 13928* (CORD, MO). Ciénaga de La Caldera, 3,600–3,650 m, *Kurtz 13935* (CORD). El Volcán, *Kurtz 14658* (CORD). Mina San Juan, 3,050–3,200 m, *Kurtz 13597, 13685* (CORD); Real Viejo, *Kurtz 14701* (CORD). Alto Blanco, *Castellanos 28-282* (POM). La

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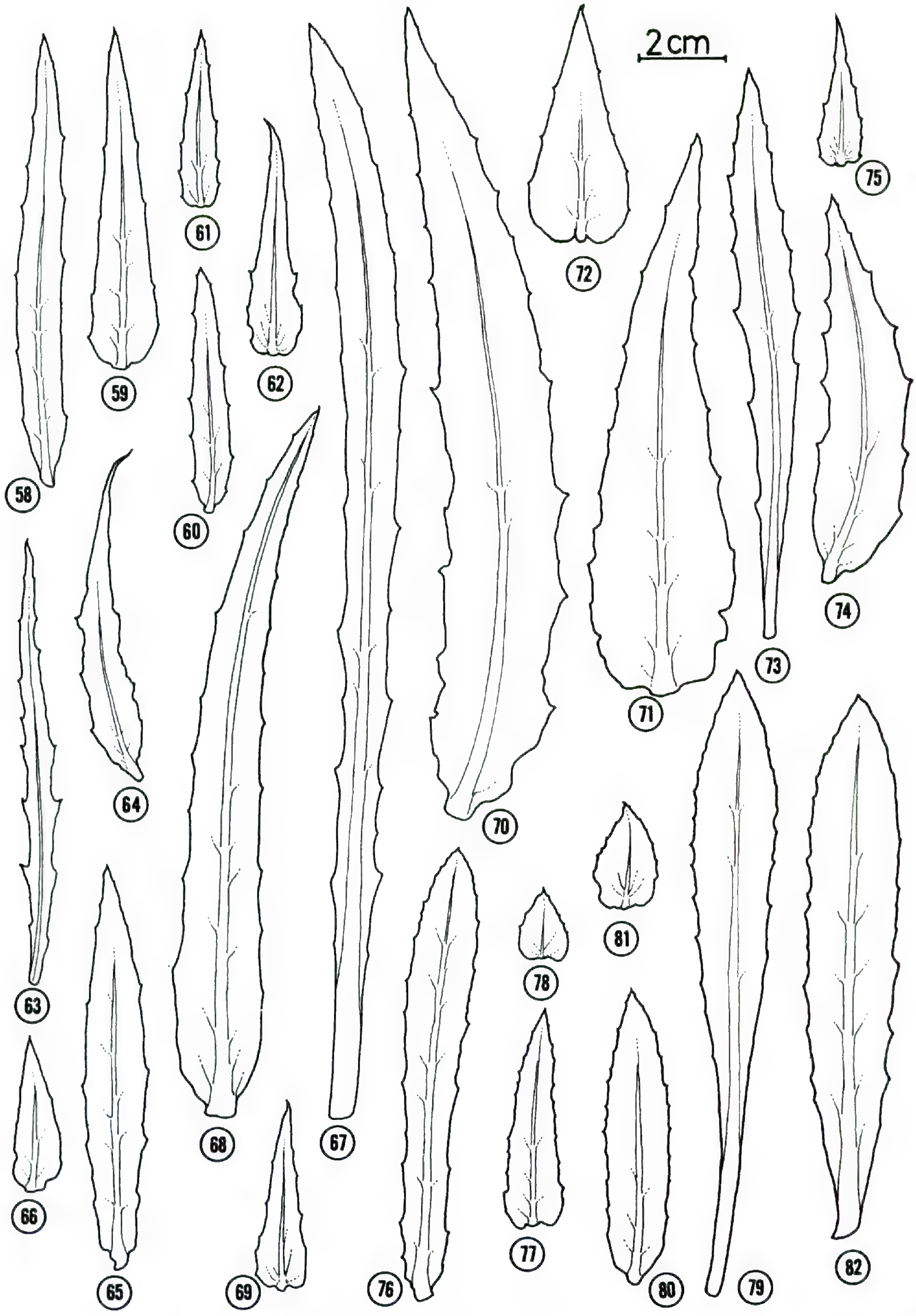
Hackbart in 1966).—44–46. Rosette leaf, cauline leaf, and bract of *O. indecora* subsp. *bonariensis* (Argentina, Corrientes, *Quarín & Schinini 1297*).—47–49. Rosette leaf, cauline leaf, and bract of *O. ravenii* subsp. *chilensis* (Chile, Cautín, *Stubbe in 1960*).—50–52. Rosette leaf, cauline leaf, and bract of *O. longiflora* subsp. *grandiflora* (Argentina, Corrientes, *Krapovickas & Cristóbal 11293*).—53–54. Cauline leaf and bract of *O. catharinensis* (Brazil, Santa Catarina, *Conrad & Dietrich 9*).—55–57. Rosette leaf, cauline leaf, and bract of *O. longiflora* subsp. *longiflora* (Uruguay, Colonia, *Santarius 73*).



Figures 58–82. Leaves of South American taxa of *Oenothera* sect. *Oenothera* (continued). —58–59. Cauline leaf and bract of *O. affinis* (Argentina, San Luis, *Conrad & Dietrich 139*). —60–61. Cauline leaf and bract of *O. mollissima* (Uruguay, Maldonado, *Santarius 161*).—62. Bract of *O. mollissima* (Uruguay, Maldonado, *Santarius 162*).—63–64. Cauline leaf and

Mejicana, 3,900 m, *Parodi 7896* (GH). Quebrada de Potrerillos, 3,800 m, *Krapovickas & Hunziker 5411, 5419* (BAB). Cueva de Perez, *Hieronymus & Niederlein 390* (CORD). Mina El Oro, *Hieronymus & Niederlein 414* (CORD). Lamadrid, Realitos, 3,800 m, *Rohmeder in 1941* (LIL). Real de los Neveros, 3,500 m (LIL-80298). Viejo, *Hossens 1422* (CORD). SAN JUAN: Cordillera del Salado, 3,800 m, *Spegazzini in 1957* (BAB). Cerro Tronador, *Spegazzini 212* pro parte (BAB).

Oenothera lasiocarpa is very closely related to *O. versicolor*, and the two are the only species of the series with pronounced red coloration of the petals. It can be separated from that species by its lower and more compact habit, erect long-villous pubescence, and dark green leaves; in *O. versicolor* the leaves are more grayish green. Small plants of *O. lasiocarpa* can also be confused with *O. nana*, but the latter does not develop a central shoot at all. Very small-leaved plants occur in *O. lasiocarpa* (e.g., *Budín 1170*), and some plants of *O. nana* growing in the area of *O. lasiocarpa* have broad leaves (*Lillo 5516*, *Rodríguez 1292*, *de la Sota 2711*) which, despite their occurrence as rosettes, resemble *O. lasiocarpa* closely. The first group of plants may be understood as occasional homozygous derivatives of *O. nana*. Similarly, the broad-leaved plants of *O. nana* may provide an indication that *O. lasiocarpa*, which is in all probability derived from *O. versicolor* in Argentina, may be involved in the origin of one of the chromosomal complexes of *O. nana*, which is always a complex heterozygote.

4. **Oenothera santarii** Dietrich, sp. nov.—FIGS. 5, 20–22, 106, 171, 195.

O. odorata Jacq. var. *brachycarpa* Haumann, Anales Soc. Ci. Argent. 86: 292. 1919. LECTOTYPE: Argentina, Prov. Mendoza, Cordilleras Altas de Mendoza, Puente del Inca to Punta de Vacas, ca. 2,500 m, Jan. 1908, *L. Haumann* (BR).

Herba annua vel biennis, rosulata, 7–12 dm alta, simplex vel caulis principalis vix ramosa, ramis arcuatis e rosula ascendentibus. Herba sparse strigulosa, aliquantum in inflorescentiam densior, et pilis erectis sparsis praedita. Folia rosulae anguste oblanceolata, acuta, lamina in petiolum gradatim decrescens, 15–30 cm longa, 2.5–4 cm lata; folia caulina angustissime elliptica, acuta, basi acuta, 10–15 cm longa, 1–2.5 cm lata, brevipetiolata vel sessilia; bractea angustissime elliptica vel lanceolata, basi attenuata vel truncata, plerumque oblique ascendentia, sessilia, 5–8 cm longa, 1–1.5 cm lata, apicibus supremarum saepe in cochleam tortis; folia valde marginibus undulatis. Inflorescentia plerumque simplex. Tubus floralis 2–2.5 cm longus. Gemmae ambito lanceolatae, 2–2.5 cm longae, 5–8 mm crassae; apices sepalorum ca. 2 mm longi, erecti. Petala latissime obovata, lutea, 2–3 cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato, vel brevis, stigmate sub anthesi antheris circumdato. Ovarium 8–10 mm longum. Capsula 2–3 cm longa, 6–9 mm crassa, maturitate fusca. Semina ± obtuse angulata, 1.2–1.4 mm longa, 0.7–1 mm lata, fusca. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

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bract of *O. rivadaviae* (Argentina, Chubut, *Santarius 913*).—65–66. Cauline leaf and bract of *O. picensis* subsp. *cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—67–69. Rosette leaf, cauline leaf, and bract of *O. stricta* subsp. *altissima* (Argentina, Río Negro, *Santarius 798*).—70–72. Rosette leaf, cauline leaf, and bract of *O. stricta* subsp. *argentinae* (Argentina, Buenos Aires, *Santarius 346*).—73–75. Rosette leaf, cauline leaf, and bract of *O. bahia-blancae* (Argentina, Buenos Aires, *Santarius 455*).—76–78. Rosette leaf, cauline leaf, and bract of *O. parodiana* subsp. *parodiana* (Argentina, Córdoba, *Conrad & Dietrich 98*).—79–81. Rosette leaf, cauline leaf, and bract of *O. parodiana* subsp. *parodiana* (Argentina, Córdoba, *Conrad & Dietrich 162*).—82. Rosette leaf of *O. parodiana* subsp. *parodiana* (Argentina, Córdoba, *Conrad & Dietrich 122*).

Erect annual or biennial herbs, forming a rosette, 7–12 dm tall. Plants unbranched or with a scarcely branched main stem and widely arcuate-ascending side branches arising from the rosette. Plant sparsely strigillose, somewhat more densely so in the inflorescence, also with sparse, erect, villous pubescence. Rosette leaves narrowly oblanceolate, acute, gradually narrowed to the petiole, 15–30 cm long, 2.5–4 cm wide; cauline leaves very narrowly elliptic, acute, acute at the base, 10–15 cm long, 1–2.5 cm wide, with a short petiole or sessile; bracts very narrowly elliptic to lanceolate, acute, acute to truncate at the base, usually obliquely ascending, sessile, 5–8 cm long, 1–1.5 cm wide, the tips of the uppermost ones often slightly spirally twisted; all leaves plane to strongly undulate at the margins and irregularly toothed. Inflorescence usually unbranched. Floral tube 2–2.5 cm long. Buds lanceolate in outline, 2–2.5 cm long, 5–8 mm thick; apices of the sepals erect, ca. 2 mm long. Petals very broadly obovate, yellow, 2–3 cm long. Anthers 9–11 mm long. Filaments 18–20 mm long. Style long, the stigma elevated above the anthers at anthesis, or short, the anthers shedding pollen directly on the stigma at anthesis, 3–5.5 cm long. Stigma lobes 3–5 mm long. Ovary 8–10 mm long. Capsule 2–3 cm long, 6–9 mm thick, brown when ripe. Seeds 1.2–1.4 mm long, 0.7–1 mm thick, more or less obtusely angular, brown. Self-compatible. Gametic chromosome number, $n = 7$ (7 bivalents* or small rings at meiotic metaphase I). Flowering time: November–March.

Type: Grown from seeds and cultivated at the Botanical Garden of Düsseldorf, Germany, 15 Aug. 1972. Source: Argentina, Prov. Mendoza, Cordillera de Los Andes, on stony places at Ruta 7, ca. 150 m E of Arroyo Santa Maria, ca. 6 km E of Puente del Inca, 2,750 m, 25 Feb. 1968, *K. A. Santarius 1430* (MO-2155403, holotype; CTES, DUSS, M, isotypes).

Distribution (Figs. 225, 241): Andes of Argentina west of Mendoza, and one locality in the province of San Juan, as well as in the Sierra de Córdoba and the Sierra de Comechingones (provinces of Córdoba and San Luis), 1,800–3,000 m elevation.

Specimens examined from cultivated plants:

ARGENTINA: MENDOZA: Cordillera de los Andes, Puente del Inca, 2,700–2,750 m, *Santarius 1405*, 1417*, 1430*, 1436*, 1443*, 1444*, 1455** (DUSS; *1430, 1435, 1436, 1455* also M; *1430, 1444* also MO). Punta de Vacas, 2,450 m, *Santarius 1492, 1500** (DUSS; *1492* also MO). Polvaredas, 2,450 m, *Santarius 1535* (DUSS, MO). SAN LUIS: Sierra de Comechingones, El Rincón, 1,500 m, *Conrad & Dietrich 152* (ring of 4 and 5 bivalents, ring of 6 and 4 bivalents) (DUSS).

Additional specimens examined:

ARGENTINA. SAN JUAN: Jáchal, Río Blanco near Punilla, *Hossens 169* (CORD). MENDOZA: Punta de Vacas, *Spegazzini in 1901* (POM), *90729, 90730* (BAB); 2,700 m, *King 695* (BM). Puente del Inca, 2,800 m, *Boelcke 9840* (BAA, BAB, MO, SI); *Spegazzini 24213* (BAB); *Wall in 1946* (S); 3,000 m, *Sparre 1644* (S); *King 430* (BAB); 2,700 m, *Ruiz Leal 6554* (LIL, Leal); *Yepes 26-762* (POM); *Gosse in 1897* (K, NY); *Malme 2858* (S); *Dawson 60* (SI). Between Puente del Inca and Las Polvaredas, *Moreau 12667* (BA). Las Heras, Arroyo Sta. Maria, 2,400 m, *Calastremé 72031* (BAB, CORD). Quebrada Sta. Maria, 2,800 m, *Hunziker 3246* (BAB, CORD). Luján, Los Vallecitos, *Ruiz Leal 22565* (Leal); 2,700 m, *Leal 13404* (Leal). Cancha de Esqui, 3,000 m, *Cuezzo & Say 2540* (LIL). Tunuyán, Quebrada Cap. Lemos, 2,300 m, *Palacios & Cuezzo 4459* (LIL). Malalhue, Tronquimalal, *Castellanos 15492* (US). CORDOBA: Sierra Grande, Valle de Los Reartes, *Castellanos 1556* (POM).

Cuesta da las Calvas, 1,800 m, *Hunziker 9682* (CORD, RSA). Pampa de Achala, near Copina, 1,900 m, *Hunziker 11912* (RSA). Sierra Achala, Cerro Los Gigantes, 2,400 m, *Doering 15659, 15647* (CORD). Copina, *Hieronymus 634* (GOET). San Javier, Loma Bela, 1,500 m, *Hunziker 8293* (CORD). Peak of the Champaquí, *Hunziker 9040* (CORD). SAN LUIS: Sierra de Comechingones, El Rincón, *Hunziker 11782* (RSA), *11789* (CORD, MO). Cerro de Piedra, *Vignati 15* (SI). Monigote, *Gerth in 1914* (L).

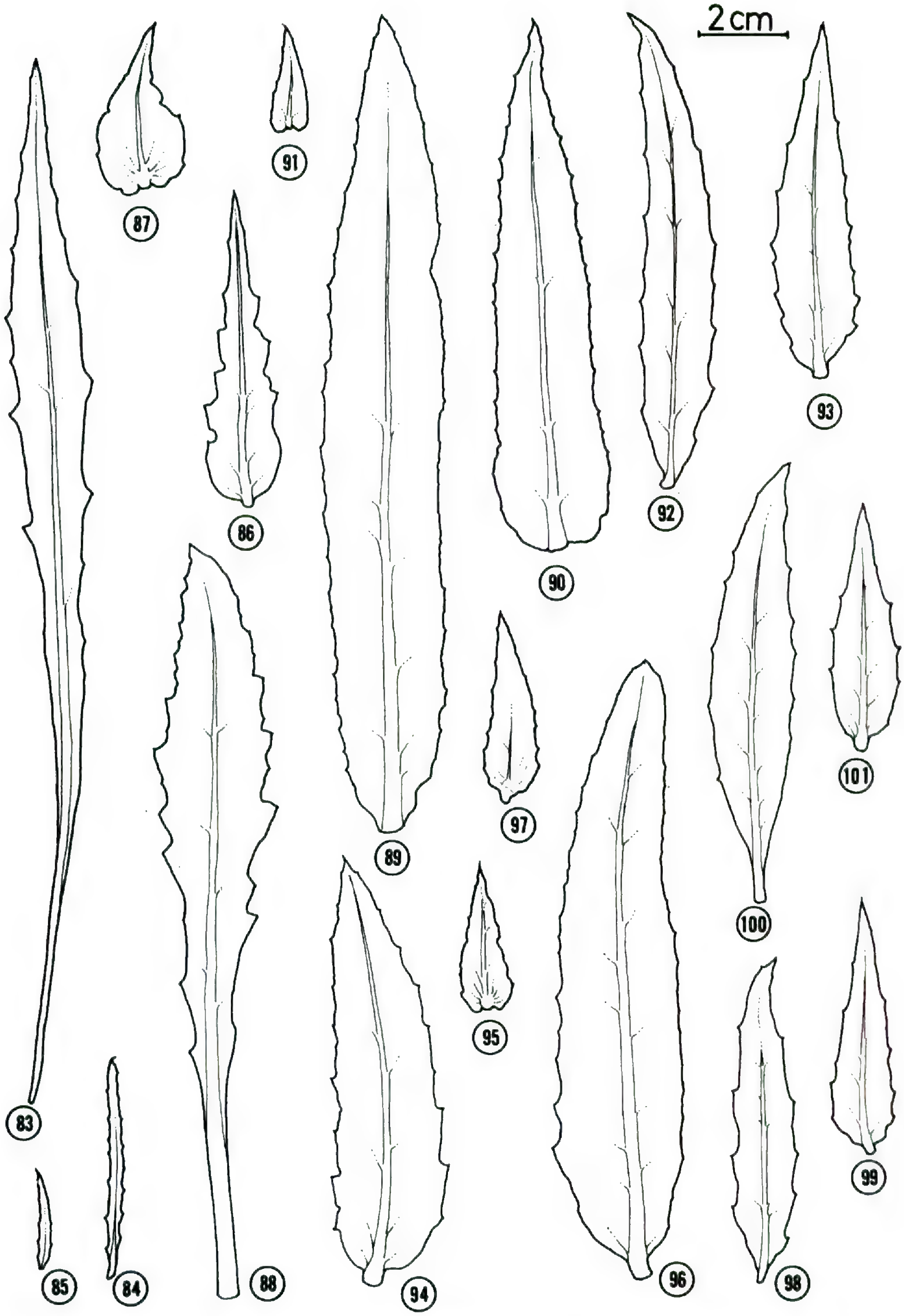
This new species is dedicated to Kurt A. Santarius (1933–), who contributed so much to this study with his extensive collections of seeds from throughout South America. It is the southernmost of the series. The very local and widely separated stations that make up its distribution are suggestive of a wider range to the north in the past. The *santarii*-complex is, however, the most widespread of all genomes of the group. *Oenothera magellanica* (*santarii–odorata*) is found throughout Argentina from Mendoza southward and southeastward to south of Punta Arenas in southernmost Patagonia; northward it radiates to the province of San Juan. As *Oenothera villaricae* (*santarii–ravenii*) the genome occurs in central Chile.

5. **Oenothera longituba** Dietrich, sp. nov.—FIGS. 25, 29–31, 107–108, 172, 196–197.

O. campylocalyx sensu Munz, Physis 11: 286. 1933, pro parte.

Herba erecta verosimiliter biennis, rosulata, 5–10 dm alta, simplex vel caulis principalis sparse ramosa et ramis lato-arcuate e rosula ascendentibus. Herba dense ad sparse strigulosam et ubique pilis longis erectis praedita, in inflorescentiam densiore pubescens. Folia rosulae anguste elliptica vel oblanceolata, acuta, lamina in petiolum brevem gradatim decrescens vel sessili, 17–35 cm longa, 2–6 cm lata; folia caulina elliptica vel ovata, acuta, basi acuta vel truncata, sessilia, 8–17 cm longa, 1.5–4 cm lata; bractea lanceolata vel ovata, acuta, basi rotundata vel subcordata, sessilia, 5–10 cm longa, 1–4 cm lata, sub anthesi maturitateque plerumque ad caulem perpendicularia. Inflorescentia plerumque simplex. Tubus floralis (5–) 7–10 cm longus. Gemmae ambito lanceolatae, 2.5–3.5 cm longae, 7–9 mm crassae, flavovirides, saepe rubrae, junctura sepalorum tubo florali anguste rubro-fasciatae; apices sepalorum 2–4 mm longi, erecti vel divergentes. Petala latissime obovata, rotundata vel retusa, 2–4 cm longa. Stylus longus, stigmata anthesi supra antheras elevata. Ovarium ca. 10 mm longum. Capsula 1.5–2.5 cm longa, 5–9 mm crassa, maturitate brunnea. Semina ± obtuse angulata, 1–1.5 mm longa, 0.5–0.6 mm lata, nigra. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Erect probably biennial herb, forming a rosette, 5–10 dm tall. Plants unbranched or with a scarcely branched main stem and widely arcuate-ascending side branches arising from the rosette. Plants densely or sparsely strigillose and with an admixture of erect villous pubescence throughout, most densely pubescent in the inflorescence. Rosette leaves narrowly elliptic or oblanceolate, acute, gradually narrowed to a short petiole or sessile, 17–35 cm long, 2–6 cm wide; cauline leaves elliptic to ovate, acute, acute to truncate at the base, sessile, 8–17 cm long, 1.5–4 cm wide; bracts lanceolate to ovate, acute, rounded to subcordate at the base, sessile, 5–10 cm long, 1–4 cm wide, in flower and fruit mostly spreading at right angles to the main stem; all leaves plane to undulate at the margins and irregularly toothed. Inflorescence usually unbranched. Floral tube (5–)7–10 cm long. Buds lanceolate in outline, 2.5–3.5 cm long, 7–9 mm thick, yellowish green, often flushed with red, narrowly red-striped at the junction of the sepals with the floral tube; apices of the sepals erect or spread-



FIGURES 83–101. Leaves of South American taxa of *Oenothera* sect. *Oenothera* (continued).—83. Rosette leaf of *O. magellanica* (Argentina, Chubut, *Santarius 1393*).—84–85. Cauline leaf and bract of *O. punae* (Argentina, Tucumán, *Krapovickas 21851*).—86–87. Cauline leaf and bract of *O. grisea* (Chile, Valparaíso, *Constance in 1965*).—88. Rosette leaf of *O. villaricae* (Chile, Cautín, *Stubbe in 1960*).—89–91. Rosette leaf, cauline leaf, and bract of

ing, 2–4 mm long. Petals very broadly obovate, rounded to retuse, 2–4 cm long. Anthers 8–12 mm long. Filaments 20–30 mm long. Style long, the stigma held above the anthers at anthesis, (6–)8–12 cm long. Stigma lobes 6–10 mm long. Ovary ca. 10 mm long. Capsule 1.5–2.5 mm long, 5–9 mm thick, dark brown when ripe. Seeds 1–1.5 mm long, 0.5–0.6 mm thick, black, ± obtusely angled. Self-compatible but outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 15 Aug. 1972. Source: Argentina, Prov. Catamarca, near La Banderita at road from Andalgala to Concepción, 1,800 m, 11 Feb. 1959, *L. Diers* (MO-2155402, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 227): Andes of Argentina and their foothills in the provinces of Jujuy, Salta, Tucumán, Catamarca, and La Rioja, 900–3,000 m elevation.

Specimens examined from cultivated plants:

ARGENTINA. JUJUY: Sierra Calilegua, Cerro Colorado, 2,900 m, *Fabris 5787** (CTES, DUSS, M, MO). TUCUMÁN: Valle de Tafí, 5 km N of Tafí del Valle, 2,000–2,250 m, *Santarius 1736**, *1737** (DUSS; *1736* also CTES, M, MO). CATAMARCA: Near La Banderita at road from Andalgala to Concepción, 1800 m, *Diers in 1959** (DUSS, M, MO).

Additional specimens examined:

ARGENTINA. JUJUY: Santa Barbara, Cerro El Centinela, *Legname & Cuezzo 5103* (LP); 2,650 m, *Fabris 5133* (LP, RSA); *Legname & Cuezzo 5199* (LIL). Valle Grande, Serrania de Calilegua, *Fabris et al. 5880* (LIL). Serrania de Calilegua, Cerro Hermosa, 2,700 m, *Fabris et al. 5391* (CTES, LP), 2,800 m, *5830* (LP). SALTA: Rosario de Lerma, Campo Tuijano, 1,500 m, *Venturi 8098* (GH, SI). La Viña, Coronel Moldes, Río Chaña Pampa, 1,200 m, *Hunziker 1068* (POM, US). TUCUMÁN: Tafí, Taficillo, 1,800 m, *Venturi 5986* (LIL, US). Yerba Buena, 750 m, *Venturi 243* (LIL, SI). San Javier, 900 m, *Venturi 243* (US); *Lillo 136* (P). Río Angostura, 1,800 m, *Sparre 1356* (S). Villa Nougués, 1,000 m, *Munz 15463* (NY, US); *Schreiter 706* (F, LIL). Infiernillo, 2,450 m, *Meyer & Vaca 23669* (LIL). Duraznillo, *Rocha 2499* (LIL). San Javier, *Rocha 870* (LIL). Tafí del Valle, 3,000 m, *Sleumer 258* (LIL). Siambón, ca. 900 m, *Munz 15470* (POM); *Lorentz 306* (CORD, GOET). Aconquija, Esquina, 1,560 m, *Lillo 1572* (LIL). Laguna del Tesoro, 2,800 m, *Türpe in 1958* (LIL). Chicligasta, Est. Los Pavos to Pto. El Bayo, 3,200 m, *Venturi 3283* (LIL), 3,000 m, *4597* (US). CATAMARCA: Andalgala, El Clavillo, 1,900 m, *Jörgensen 1560* LIL, SI, US). Andalgala, Río Vallecito, 2,500 m, *Rohmeder in 1942* (LIL). Yacutula near Belén, *Schickendantz 114* (CORD). LA RIOJA: Sierra de Famatina, La Hoyada, 2,500 m, *Kurtz 15042, 15044* (CORD, MO). Sierra Velasco, Yacuchi, *Kurtz 15367* (CORD). Sarmiento, Juntas del Bonete and Ciénaga Grande, *Krapovickas & Hunziker 5909* (BAB).

Oenothera longituba is unmistakable because of its sturdy rosette and the long floral tubes that elevate the mature buds and flowers above the apex of the stem. Its genome has been involved in the origin of several complex structural heterozygotes, namely *O. tarijensis* (*versicolor–longituba*), *O. recurva* (*longituba–scabra*); it is also present in the predominantly Peruvian *O. weberbaueri*, so that this genome or at least one very similar must have been playing an active

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O. hechtii (Argentina, Tucumán, *Hecht 1964-81*).—92–93. Cauline leaf and bract of *O. acuticarpa* (Argentina, Tucumán, *Göpel in 1961*).—94–95. Cauline leaf and bract of *O. cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—96–97. Cauline leaf and bract of *O. siambonensis* (Argentina, Tucumán, *Hecht 1964-84*).—98–99. Cauline leaf and bract of *O. tucumanensis* (Argentina, Tucumán, *Santarius 1657*).—100–101. Cauline leaf and bract of *O. brevipetala* (Bolivia, Cochabamba, *Santarius 1972*).

role at least as far as Peru in the past. The genome of *O. longituba* has also entered into combinations with *O. affinis* and *O. ravenii* of series *Allochroa*, and from these combinations *O. elongata* and *O. hechtii*, which belong to series *Clelandia*, have arisen.

On the basis of the striking similarity in habit with *O. longiflora* and *O. ravenii*, it can be concluded that these species may have originated from an ancestor that resembled *O. longituba*.

6. **Oenothera tafiensis** Dietrich, sp. nov.—FIGS. 17–19, 23, 109–110.

Herba erecta annua vel biennis, rosulata, 4–10 dm alta, simplex vel caulis principalis crassus vel gracilis et ramis arcuate e rosula ascendentibus. Herba dense vel densissime strigulosa, etiam in inflorescentiam appresse villosa. Folia rosulae anguste elliptica vel anguste oblanceolata, acuta, lamina in petiolum gradatim vel ± abrupte decrescens, 15–20 cm longa, 1.5–2.5 cm lata; folia caulina anguste elliptica vel anguste lanceolata, acuta, basi anguste cuneata vel anguste lanceolata, 5–13 cm longa, 1–2 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi acuta vel truncata, sessilia, 5–8 cm longa, 1–2 cm lata; folia irregulariter obtuseque serrata. Inflorescentia plerumque simplex. Tubus floralis 2.5–5.5 cm longus. Gemmae ambito oblongae vel lanceolatae, 1.5–3 cm longae, 5–7 mm crassae, cinereo-virides vel flavescentes, junctura sepalorum tubo florali anguste rubro-fasciatae; apices sepalorum ca. 2 mm longi, erecti vel divergentes. Petala latissime obovata, retusa, 1.5–4 cm longa. Stylus brevis, stigmata anthesi antheribus circumdato. Ovarium 8–10 mm longum. Capsula 1.5–3 cm longa, 5–9 mm crassa, brunnea punctibus rubro-fuscis maculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Erect annual or biennial herbs, forming a rosette, 4–10 dm tall. Plants unbranched or with a very thick to slender main stem and arcuately ascending side branches arising from the rosette. Entire plant densely to very densely strigillose with an admixture of appressed long-villous pubescence in the inflorescence. Rosette leaves narrowly elliptic to narrowly oblanceolate, acute, gradually or ± abruptly narrowed to the petiole, 15–20 cm long, 1.5–2.5 cm wide; cauline leaves narrowly elliptic to narrowly lanceolate, acute, narrowly cuneate to narrowly lanceolate at the base, 5–13 cm long, 1–2 cm wide; bracts narrowly lanceolate to lanceolate, acute, acute to truncate at the base, sessile, 5–8 cm long, 1–2 cm wide; leaves usually plane at the margins, irregularly and bluntly serrate. Inflorescence usually unbranched. Floral tube 2.5–5.5 cm long. Buds oblong to lanceolate in outline, 1.5–3 cm long, 5–7 mm thick, gray green or yellowish, red striped at the junction of the sepals with the floral tube; apices of the sepals erect or spreading, ca. 2 mm long. Petals very broadly obovate, retuse, 1.5–4 cm long. Anthers 6–15 mm long. Filaments 12–30 mm long. Style short, the anthers usually shedding pollen directly on the stigma at anthesis, 3.5–8.5 cm long. Stigma lobes 3–8 mm long. Ovary 8–10 mm long. Capsule 1.5–3 cm long, 6–8 mm thick, dark gray brown when ripe. Seeds elliptic, 1–1.2 mm long, 0.5–0.6 mm thick, brown, flecked with dark reddish brown. Modally self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: northern area, December–May; southern area, December–March.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 25 July 1972. Source: Argentina, Prov. Tucumán, bed of Río Angostura from Tafí del Valle upstream for ca. 5 km N, mostly gravel, ca. 2,000–

FIGURES 102–105. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—102. *O. peruana* (Peru, Arequipa, *Santarius 2096*).—103. *O. versicolor* (Peru, Junín, *Santarius 2163*).—104. *O. versicolor* (Bolivia, Cochabamba, *Diers in 1959*).—105. *O. lasiocarpa* (Argentina, Tucumán, *Diers in 1959*).

2,250 m, 10 Mar. 1968, *K. A. Santarius 1735* (MO-2155400, holotype; DUSS, M, MO, isotypes).

Distribution (Figs. 228–229): Andes and Sierra de Córdoba of Argentina in the provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, and Córdoba, 1,500–3,000 m elevation.

Oenothera tafiensis can be separated from the very similar *O. scabra* by its entirely appressed pubescence.

KEY TO THE SUBSPECIES

1. Buds 2–3 cm long, lanceolate in outline; apices of the sepals erect; petals 2–4 cm long .... 6a. subsp. *tafiensis*

1'. Buds 1–1.5 cm long, oblong in outline; apices of the sepals divergent; petals 1.5–2 cm long .... 6b. subsp. *parviflora*

6a. **Oenothera tafiensis** subsp. **tafiensis**.—FIGS. 17–19, 109.

O. campylocalyx sensu Munz, Physis 11: 289. 1933, pro parte.
O. campylocalyx sensu Descole, Gen. Sp. Pl. Argent. 2: *tab. 164.* 1944.

Main stem unbranched or branched and with arcuate-ascending side branches arising from the rosette. Rosette leaves narrowly lanceolate, gradually narrowed to the petiole. Floral tube 2.5–5 cm long. Buds lanceolate in outline, 2–3 cm long, gray green; apices of the sepals erect. Petals 2–4 cm long. Anthers 10–15 mm long. Filaments 15–30 mm long. Style 3.5–8.5 cm long. Stigma lobes 5–8 mm long.

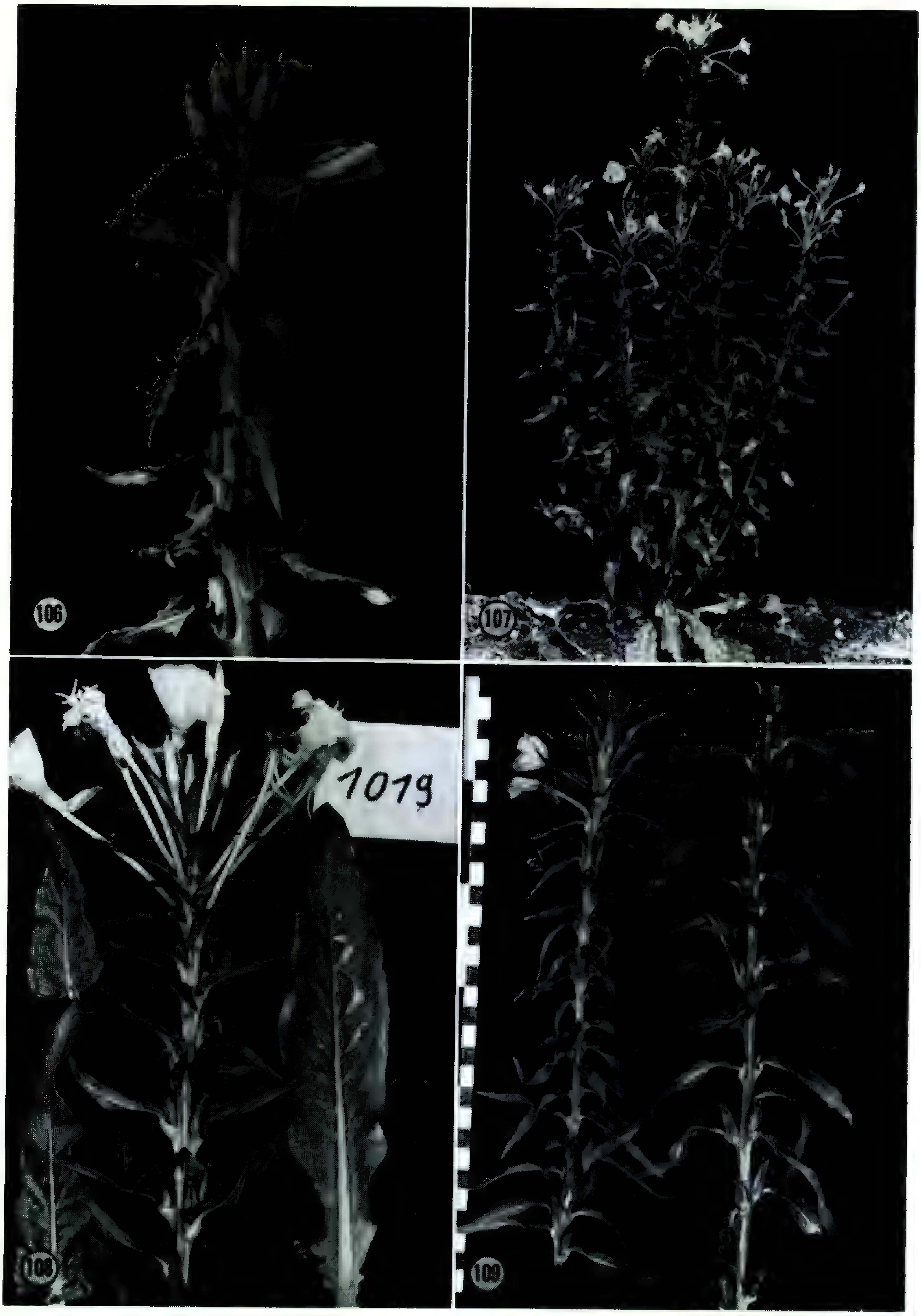
Distribution (Fig. 228): As in the species.

Specimen examined from cultivated plants:

ARGENTINA. TUCUMÁN: Bed of Río Angostura, 5 km N of Tafí del Valle, 2,000–2,250 m, *Santarius 1733, 1735*, 1739*, 1741** (DUSS; *1735* also M; *1733, 1735* also MO).

Additional specimens examined:

ARGENTINA. JUJUY: Termas de Reyes, *Hunziker 26196* (RSA); *Romero in 1947* (LIL). Laguna Yala, 2,100 m, *Romero in 1947* (LIL); *O'Donnell 4832* (LIL); *Cabrera et al. 21273* (LP). Tumbaya, Volcán, Chilcayo, *Cabrera 18207* (LP). Volcán, *Romero in 1947* (LIL). Est. Volcán, 2,100 m, *Castillon 322* (LIL). Valle Grande, Serrania de Calilegua, Mesias, *Fabris et al. 5858* (LIL). Guachipas, between Pampa Grande and El Lajar, *Meyer 21940* (LIL). SALTA: Cachi, peak of Obispo, *Romero in 1947* (LIL). San Fernando to the peak of Obispo, *Meyer 12481* (LIL). Cachi, Adentro, *Romero in 1947* (LIL). El Alisal, Cerro de Capán, 2,800 m, *Rodriguez 1298* (LIL, POM, SI). Sierra de la Candelaria, 2,200 m, *Venturi 3811* (BAB, LIL, SI, US). Slope of Unquillo near Candelaria, 2,000 m, *Schreiter 9435* (LIL). San Pedro near Truya, 3,000 m, *Petersen & Hjerting 224* (C, LIL). TUCUMÁN: Anfama, *Monetti 288* (BAB). Valle de Tafí, *Bruch in 1908* (LP, NY, RSA); *Türpe in 1959* (LIL). La Escorzonera, 2,000 m, *Lourteig 480, 496* (LIL). La Quebradita, 2,000 m, *Lourteig 484* (LIL). Tafí, Valdas del Cerro, 2,000–3,000 m, *Lourteig 528* (LIL). Quebrada de Mastil, 2,200 m, *De La Sota 155* (LIL). La Ciénaga, *Descole 1529* (LIL); *Lillo 4008, 4020* (LIL); *Lorentz & Hieronymus* 688 (GOET). Tafí, *Dinelli 597* (BAB). Sierra del Cajón, La Silla, 3,000 m, *Venturi 4504* (LIL). Tafí, 2,000 m, *Sparre 5648* (LIL). Chaquivil, *Olea 180* (LIL). Tafi-cillo, *Olea in 1945* (LIL). Tafí, Río Churqui, 2,000 m, *Schreiter 1275* (LIL). Cerro San Javier, 1,200 m, *Lillo 367* (LIL). Matorrales, 2,000 m, *Lillo 3039* (LIL). Anfama, 2,500 m, *Lillo 3985* (GH, LIL, POM, UC). Tafí, *Lillo 3547, 3102, 4109, 4287* (LIL), *4311* (F, LIL), *7452* (F, LIL, POM, US). Río Blanco, 2,600 m, *Lillo 4266* (LIL). Río del Churqui, 2,010 m, *Lillo 7511* (LIL). Slope of Malamala, 2,400 m, *Lillo 3417* (LIL), 2,800 m, *4357* (LIL). Siambón, El Matadero, 1,100 m, *Lillo 1770* (LIL). Siambón, 2,100 m, *Lillo 1772* (LIL). Chicligasta, Est. Las Pavas, 2,600 m, *Lillo 4135* (LIL). Chicligasta, between La Cascada and



FIGURES 106–109. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munia*.—106. *O. santarii* (Argentina, Mendoza, *Santarius 1430*).—107. *O. longituba* (Argentina, Catamarca, *Diers in 1959*).—108. *O. longituba* (Argentina, Catamarca, *Diers in 1959*).—109. *O. tafiensis* subsp. *tafiensis* (Argentina, Tucumán, *Santarius 1735*).

Las Cuevas, 3,000 m, *Meyer 14957* (LIL, RSA). Burroyacú, Cerro del Campo, 2,500 m, *Bailletti 8* (GH, LIL); *Stuckert 22000* (CORD). Aconquija, 1,560 m, *in 1890* (LIL). Trancas, 1,950 m, *N.N. 276* (LIL). CATAMARCA: Andalgala, *Jörgensen 1054* pro parte (US), *1058* pro parte (GH, MO, SI). El Suncho, 2,500 m, *Jörgensen 1058* (US). Andalgala, "Las Mesadas," 1,650 m, *Pedersen & Hjerting in 1949* (C); *Brücher in 1949* (LD). Río Vallecito, 2,500 m, *Rohmeder in 1942* (LIL). Río Potrero, 2,600 m, *Rohmeder in 1942* (LIL). Los Quenoales, Mesada de las Rosas, 2,500–2,700 m, *Sleumer 2241* (LIL). Yunka Suma, *Meyer 14718* (LIL). Santa Maria, Sierra de Anconquija, 3,100 m, *Peirano in 1933* (LIL). Cuesta Muschaca, *Schickendantz in 1876* (CORD). El Rodeo, *Mawecin 26* (CORD). Pomán, Cerro Manchado, 2,500–2,750 m, *Hunziker & Ariza 20507* (CORD). LA RIOJA: Sierra Velazco, Yacuchi, 2,100 m, *Kurtz 15384* (CORD). Velazco, 2,200 m, *Soriano 1003* (SI). Sierra de Famatima, La Mesada, 3,500 m, *Kurtz 13837* (CORD). CÓRDOBA: Valle de los Reartes, *Hicken 94* (SI); *Castellanos in 1920* (LIL), *94* (SI). Est. San Bernardo, 1,400 m, *Hunziker 12056* (CORD), *12006* (RSA). Colón, Salsipuedes, *Dawson 84* (NY). Valle de Punilla, Capilla del Monte, road to Huertas Malas, *Hossens 416* (CORD).

At least in cultivation, the first five species listed all form a heavy rosette first. From this rosette subsequently arises the main shoot and several side branches. *Oenothera tafiensis* subsp. *tafiensis* is different in this respect, since the rosette often sprouts near the base of the main shoot, without forming branches itself. Since the rosette leaves, coming in contact with the ground, soon rot, the plant soon assumes the habit of the early-bolting *O. scabra*. In addition, the flecked seeds suggest that *O. tafiensis* occupies a position intermediate between the rosette-forming and the early-bolting species, which are probably to be regarded as derivative species in view of the fact that they are obligate annuals.

6b. **Oenothera tafiensis** subsp. **parviflora** Dietrich, subsp. nov.—FIGS. 23, 110.

Plantae nunquam e rosula compacta foliosa rames facientes, ad finem caulem principalem simplicem vel 1–3-ramosem producti. Folia rosulae ellipticala, lamina in petiolum ± gradatim decrescens, 6–8 cm longa, 1–1.5 cm lata. Tubus floralis 4–5.5 cm longus. Gemmae ambito oblongae, 1–1.5 cm longae, flavovirides, junctura sepalorum tubo florali rubro-fasciatae; apices sepalorum divergentes. Petala 1.5–2 cm longa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Plant never forming side branches from the compact, leafy rosette, but ultimately elongating and forming a main stem which is either unbranched or has 1–3 side branches. Rosette leaves elliptical, ± abruptly narrowed to the petiole, 6–8 cm long, 1–1.5 cm wide. Floral tube 4–5.5 cm long. Buds oblong in outline, 1–1.5 cm long, yellowish green, red striped at the junction of the sepals with the floral tube; apices of the sepals divergent. Petals 1.5–2 cm long. Anthers 6–7 mm long. Filaments 12–16 mm long. Style 5–7 cm long. Stigma lobes 3–4 mm long. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botnical Garden of Düsseldorf, Germany, 25 July 1972. Source: Argentina, Prov. Tucumán, Villa Nougés near Tucumán, *G. Göpel in 1961** (MO-2155397, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 229): Known only from the type locality.

Specimens examined from cultivated plants: *Göpel in 1961** (DUSS, M, MO).

FIGURES 110–113. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—110. *O.* ***tafiensis*** subsp. *parviflora* (Argentina, Tucumán, *Göpel in 1961*).—111. *O.* ***pedunculifolia*** (Argentina, Tucumán, *Santarius 1745*).—112. *O. pedunculifolia* (Argentina, Tucumán, ***Santarius*** *1745*).—113. *O. scabra* (Bolivia, Cochabamba, *Santarius 2003*).

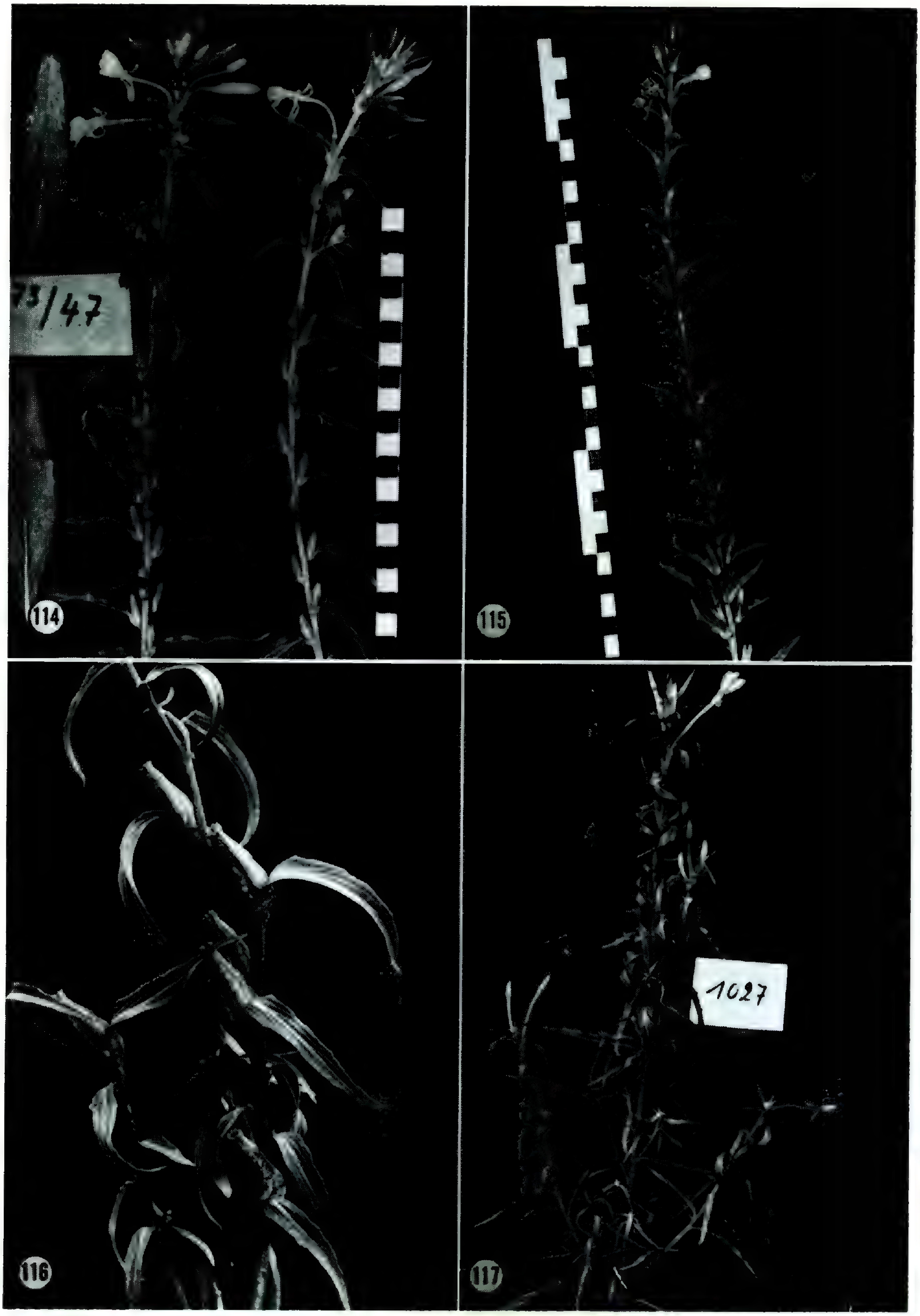
This strain, which I consider so closely related to *O. tafiensis* that the two are best regarded as subspecies of a single species, seems to have contributed its genome to *O. acuticarpa*, a species that has derived its second genome from *O. affinis*. *Oenothera tafiensis* subsp. *parviflora* and *O. acuticarpa* both were collected by Mr. G. Göpel at the same locality. When plants of *O. acuticarpa* are self-pollinated in cultivation, chromosomally homozygous individuals typical of *O. tafiensis* subsp. *parviflora* appear in the progeny, but none representative of the genome derived from series *Allochroa* specifically *O. affinis*. See also the remarks under *O. acuticarpa*.

7. **Oenothera pedunculifolia** Dietrich, sp. nov.—Figs. 32–34, 111–112, 198.

Herba annua rosulata, 7–12 dm alta, caulis principalis ± ramosus, e rosula ramis nullis. Planta dense solumque strigulosa. Folia rosulae oblanceolata vel anguste obovata, breviter acuta, lamina in petiolum gradatim decrescens, 15–20 cm longa, 3–4(–5) cm lata; folia caulina anguste elliptica vel elliptica, acuta, basi anguste cuneata, petiolata, 6–15 cm longa, 2–4(–5) cm lata; bractea anguste elliptica, acuta, basi anguste cuneata, petiolata, 5–8 cm longa, 1.5–2.5 cm lata; folia laete virides, ± regulariter acuteque serrata. Inflorescentia plerumque simplex, floribus confertissima, quum flores aetatem 4–6 dies attingentes habeant perfecte elongata. Tubus floralis 2.5–5.5 cm longus. Gemmae ambito anguste lanceolatae vel lanceolatae, flavidae, 2–3 cm longae, 5–7 mm crassae; apices sepalorum 2.5–3.5 mm longi, erecti vel divergentes. Petala latissime obovata, retusa, 2–4 cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato. Ovarium 7–9 mm longum. Capsula 1.5–2 cm longa, 4–5 mm crassa. Semina ambito elliptica vel late elliptica, 0.8–1 mm longa, 0.4–0.5 mm lata, plerumque porphyrio punctulata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Erect annual herb, forming a rosette, 7–12 dm tall. Rosette giving rise to a ± branched main stem, but never with basal shoots from the rosette. Entire plant densely and exclusively strigillose. Rosette leaves oblanceolate to narrowly obovate, short-acute, ± abruptly narrowed to the petiole, 15–20 cm long, 3–4(–5) cm wide; cauline leaves narrowly elliptic to elliptic, acute, narrowly cuneate at the base, petiolate, 6–15 cm long, 2–4(–5) cm wide; bracts narrowly elliptic, acute, narrowly cuneate at the base, petiolate, 5–8 cm long, 1.5–2.5 cm wide; leaves bright green, ± plane at the margins and ± regularly and sharply serrate. Inflorescence mostly unbranched, very thick-set with flowers, with 4–6 flowers opening per day. Floral tube 2.5–5.5 cm long. Buds narrowly lanceolate to lanceolate in outline, yellowish, 2–3 cm long, 5–7 mm thick; apices of the sepals erect or spreading, 2.5–3.5 mm long. Petals very broadly obovate, retuse, 2–4 cm long. Anthers 7–10 mm long. Filaments 15–20 mm long. Style long, the stigma held above the anthers at anthesis. Stigma lobes 4–5.5 cm long. Ovary 7–9 mm long, 3.5–6.5 cm long. Capsule 1.5–2 cm long, 4–5 mm thick. Seeds elliptic to broadly elliptic in outline, 0.8–1 mm long, 0.4–0.5 mm thick, usually flecked with dark reddish brown. Self-compatible but modally outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: December–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 24 July 1973. Source: Argentina, Prov. Tucumán, Valle de Tafí, at km 46 of Ruta 307, 15 km before Tafí del Valle, 1,800 m, 12 Mar. 1968, *K. A. Santarius 1745* (MO-2155702, holotype; CTES, DUSS, M, isotypes).



FIGURES 114–117. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—114. *O. scabra* (Peru, Ayacucho, *Santarius 2251*).—115. *O. rubida* (Peru, Arequipa, *Santarius 2101*).—116. *O. tarijensis* (Bolivia, Tarija, *Santarius 1924*).—117. *O. recurva* (Bolivia, Tarija, *Santarius 1955*).

Distribution (Fig. 230): Foothills of the Andes in the provinces of Tucumán and Catamarca, Argentina, 1,500–2,000 m elevation.

Specimens examined from cultivated plants:

ARGENTINA. TUCUMÁN: Valle de Tafí, 1500–1800 m, *Santarius 1745*, 1747*, 1754*, 1760, 1762*, 1769*, 1781*, 1785, 1786** (DUSS; *1747, 1781* also CTES; *1745, 1747, 1781* also M; *1745, 1747, 1754, 1769, 1781, 1786* also MO).

Additional specimens examined:

ARGENTINA. TUCUMÁN: Valle de Tafí, *Bruch in 1908* (NY); *Diers 320* (SI). Villa Nougés, 1,000 m, *Venturi 2418* (BAB, GH, LIL, POM, SI, US), *204* (POM). Aconquija, Esquina Grande, 1,560 m, *Lillo 1570* (LIL). Malamala, 1,950 m, *N.N. in 1901* (LIL-80370). Cerro de Garabatal near Siambón, *Lorentz & Hieronymus 854* (CORD, GOET). Río Cochuna, 1,700 m, *Schreiter 10481* (F, LIL). Dep. Monteros, Río de los Sosas, km 33 "La Heladera," *Jones 10380* (BAA). Dep. Chicligasta, Las Lagunas near Clavillo, ca. 1,680 m, *Munz 15467* (F, GH, NY, POM, US). CATAMARCA: El Candado, *Jörgensen 1058* pro parte (LIL). El Clavillo near Andalgala, *Jörgensen 1560* pro parte (MO). Río Prisavil, 1,600 m, *Brücher in 1949* (LD, S).

Like *O. tafiensis*, *O. peduncülifolia* is in some respects intermediate between the potentially biennial (species 1–5) and strictly annual (species 8) members of the subsection. In contrast to all other species of the group, *O. pedunculifolia* always has clearly petiolate bracts. In habit and probably also in actual relationship it seems closest to *O. tafiensis*, from which it can be separated by its better developed branching; sharply toothed leaves; bright green hue, in contrast to the gray green of *O. tafiensis*; and shorter capsules.

Hybrids between these two species have been found. The progeny of *Santarius 1781* included an intermediate plant which had a ring of 6 and 4 bivalents in meiosis. Some intermediate plants, on the other hand, are chromosomally homozygous (e.g., *Santarius 1747*), which suggests that populations of the two species exist with undifferentiated chromosomal end arrangements.

8. **Oenothera scabra** Krause, Repert. Spec. Nov. Regni Veg. 1: 168. 1905.—FIGS. 9, 28, 113–114, 173, 199–200.

O. campylocalyx sensu Munz & Johnston, Contr. Gray Herb. 75: 22. 1925, pro parte.
O. campylocalyx sensu Macbride, Field. Mus. Nat. Hist., Bot. Ser. 13(4): 535. 1941, pro parte.
O. burkartiana Bartlett, Darwiniana 6: 208. 1943. TYPE: Argentina, Prov. Salta, Dep. Guachipas, "Pampa Grande," 1,600 m, 27 Apr. 1942, *A. T. Hunziker 1738* (SI, holotype; CORD, LIL, isotypes).
O. curvifolia Fischer, Feddes Repert. Spec. Nov. Regni Veg. 64: 235. 1962. TYPE: Cultivated in the Botanical Garden of Erlangen, *Fischer* (ER).
O. curvifolia "Erlangen" Cleland, Jap. J. Genet. 43: 332. 1968.

Erect annual herb, not forming a rosette, 4–15 dm tall. Main stem unbranched or moderately to extensively branched. Entire plant densely, sparsely, or not strigillose, thickly to sparsely clothed with erect, long-villous pubescence, and often also somewhat glandular-pubescent. Cauline leaves very narrowly elliptic to elliptic or narrowly lanceolate to narrowly ovate, acute, acute to obtuse at the base, sessile or short-petiolate, 5–15 cm long, 1–4 cm wide; bracts narrowly elliptic to oblanceolate, acute, acute to obtuse at the base, sessile or very shortly petiolate, 4–10 cm long, 1–3 cm wide; leaves plane or evidently undulate at the margins, ± regularly or irregularly and sinuately serrate, the teeth blunt. Inflorescence branched or not. Flowers seldom or never overtop-

FIGURES 118–119. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia.*—118. *O. sandiana* (Peru, Cuzco, *Santarius 2307*).—119. *O. sandiana* (Bolivia, La Paz, *Santarius 2018*).

ping the apex of the stem. Floral tube 2.5–5(–7.5) cm long. Buds narrowly oblong to oblong or narrowly lanceolate to lanceolate in outline, 1–3.5 cm long, 4–6 mm thick, yellowish green, often red striped at the junction of the sepals with the floral tube; apices of the sepals erect or spreading, 1–3 cm long. Petals very broadly obovate, usually retuse, yellow, 2.5–3.5 cm long. Anthers 5–11 mm long. Filaments 8–25 mm long. Style long, the stigma elevated above the anthers at anthesis, or short, the anthers shedding pollen directly on the stigma at anthesis, 3.5–8(–9.5) cm long. Stigma lobes 3–6 mm long. Ovary 5–10 mm long. Capsule 1.5–2.5 cm long, 5–7 mm thick. Seeds 0.8–1.3 mm long, 0.4–0.6 mm thick, elliptic to broadly elliptic in outline, brown, often flecked with dark reddish brown. Self-compatible; modally outcrossing or self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents* or ring of 4 and 5 bivalents** at meiotic metaphase I). Flowering time: December–May.

Type: Bolivia, Dep. Tarija, shrubby places along a stream, 2,000 m, 30 Dec. 1903, *K. Fiebrig 2434* (B, destroyed in World War II, UC-292686-7 fragments and photographs, F and POM photographs; G, K, L, LY, isotypes).

Distribution (Fig. 231): Andes from the department of Ayacucho in Peru to the province of La Rioja in Argentina, 1,000–3,200 m elevation.

Specimens examined from cultivated plants:

PERU. AYACUCHO: Ucros, about 116 km behind Ayacucho at road to Andahuaylas, 3,150 m, *Santarius 2251** (CTES, DUSS, M, MO).

BOLIVIA. COCHABAMBA: Incachaca, 2,250 m, *Santarius 2003**, *2007** (DUSS, M, MO; *2003* also CTES).

ARGENTINA. JUJUY: Quebrada de Yala, 1,700 m, *Diers in 1959** (CTES, DUSS, M, MO). CATAMARCA: Dep. Ambato, Ruta 62, 19 km N of Singuil, *Hunziker 9181*** (CTES, DUSS, M, MO).

CULTIVATED: *O. scabra* from Erlangen, received 1960* (CTES, DUSS, M, MO). *O. curvifolia* from Erlangen, received 1962* (CTES, DUSS, M, MO).

Additional specimens examined:

PERU. AYACUCHO: Allate, *Soukup 481* (F). CUZCO: Ollantaytambo, 3,000 m, *Cook & Gilbert 294* (US). PUNO: Carabaya near Antapampa, 4,180 m, *Vargas 7002* pro parte (LIL). MOQUEQUA: Carumas, 3,000 m, *Weberbauer 7283* (BM, F, POM, S, US).

BOLIVIA. LA PAZ: Titicaca, *N.N.* (K). Titicaca, Isla del Sol, 3,840 m, *Buchtien 4661* (US). Larecaja, vicinity of Sorata, 2,690–3,000 m, *Mandon 627* (GH, pro parte, P, W), 3,200 m, *628* (BM, K, LE, P, S, W). COCHABAMBA: Chapare, Incachaca, 2,200 m, *Steinbach 9145* (BM, F, G, GH, K, LIL, MO, NY, S). ORURO: Choro, ca. 2,130 m, *Brooke 6128* (BM). CHUQUISACA: Serrano, *Cárdenas 4114* (US). TARIJA: Tucumilla, 2,800 m, *Fiebrig 3351* (P). Vicinity of Tarija, 1,700 m, *Zelada 40* (LIL).

ARGENTINA. JUJUY: Dep. Capital, Lagunas de Yala, *Cabrera & Fabris 17478* (BAA, LP); *Cabrera et al. 21318* (LP). Yala, 2,086 m, *Romero 34* (LIL). Termas de Reyes, *Romero in 1947* (LIL). Almiron Luzano, *N.N. 88* (LIL-347275). Tumbaya, Volcán Chilcayo, 2,300 m, *Fabris 6089* (BAA). Santa Barbara, Los Monteros, *Cabrera 5205* (LP). Valle Grande, 2,600 m, *Burkart 115959* (SI). Río Chico, 1,258 m, *Schreiter 2834* (LIL). SALTA: La Ollada, *Lahitte 49842* (BAB). Orán, San Andres, 1,800 m, *Pierotti 294* (LE, LIL, NY, UC), *1378* (LIL, NY, UC). Río Cañas near Orán, *Willirich 351* (LIL). Valle de Lerma, *Tabala 17* (LIL). Campo Quijano, Río Toro, *Krapovickas 10051* (LIL). TUCUMÁN: Tafí, *Lillo 4155* (LIL, MO). Las Peñas Azules, 3,200 m, *Olea in 1933* (S). San Javier, *Rocha 1001* (LIL). Río Chico, Escaba, 2,250 m, *Monetti 1841* (GH), *14900* (LIL). Burroyacú, Duraznillo, 1,000 m, *Monetti 2051* (GH). CATAMARCA: Andalgala, *Jörgensen 1560* pro parte (GH). Between Andalgala and Capillitas, *O'Donell & Meyer 5215* (LIL). Huillapima, *Spegazzini 28673* (BAB). Sierra de Ambato, Casa de Cubas to Las Lajas, 3,300 m, *Hunziker et al. 20086* (CORD). Pomán, Las Ciénagas, 2,000 m, *Vervoorst 3503* (LIL). Pomán, Sierra de Ambato, Cerro Manchado, 2,500–2,750 m, *Hunziker 20465* (CORD, MO). LA RIOJA: Sierra de Famatima, Chilecito, Mina El Oro, 3,000 m, *Calderon 1079* (BAA).

Oenothera scabra never forms a rosette, but grows soon after germination from only a few basal leaves to an erect, often well-branched, plant. Another characteristic is the erect villous pubescence.

Even though there is a considerable amount of natural variation, it is not possible to delimit taxonomically useful races within *O. scabra*. There are plants of *O. scabra* (e.g., *Cárdenas 4114*, *Hunziker 9181*) that totally lack the strigillose pubescence otherwise found in all species of series *Renneria*. They are therefore exclusively villous and glandular-pubescent, a characteristic that otherwise occurs only in the species of series *Allochroa* and *Clelandia*. Since, in addition the capsule may often be broadly cylindrical, one is led to the conclusion that *O. scabra* may be closely related not only to *O. affinis*, which has large flowers and a long floral tube, but also to the small-flowered *O. indecora*. Both are exclusively villous and glandular-pubescent.

9. **Oenothera rubida** Rusby, Bull. New York Bot. Gard. 8: 110. 1912.—FIG. 115.

O. laciniata sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 537. 1941, pro parte.

Erect annual herb, not forming a rosette, 5–10 dm tall. Plants branched from the base upward. Entire plants densely strigillose, and also erect long-villous in the region of the inflorescence. Cauline leaves very narrowly elliptic to narrowly elliptic, acute, narrowly cuneate at the base, short-petiolate, 2.5–7 cm

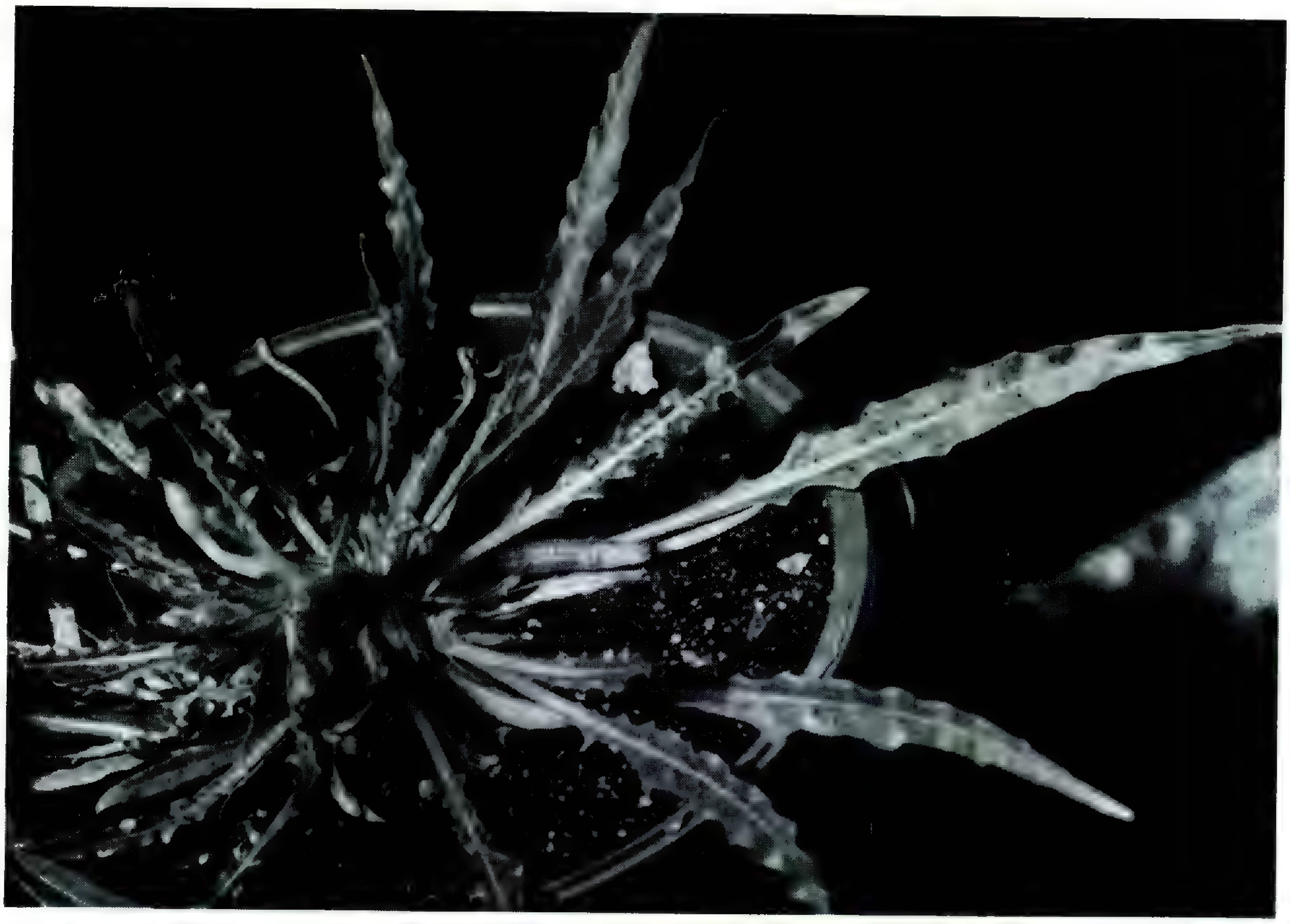


FIGURE 120. *Oenothera nana* (Argentina, Jujuy, *Santarius 1895*); *Oenothera* sect. *Oenothera* subsect. *Munzia*.

long, 0.5–1.5 cm wide; bracts narrowly elliptic to lanceolate, acute, acute to truncate at the base, sessile or very short-petiolate, 3–7 cm long, 1–2 cm wide; leaves usually undulate at the margins and ± regularly and sharply serrate. Inflorescence simple or branched. Floral tube 1–2 cm long. Buds oblong to narrowly ovate in outline, ca. 1 cm long, 4–5 mm thick; apices of the sepals erect or divergent, 2–3 mm long. Petals very broadly obovate, 0.8–1.2 cm long. Anthers 4–6 mm long. Filaments 6–8 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.5–2.8 cm long. Stigma lobes 3–5 mm long. Ovary 8–10 mm long. Capsule 1.8–2.5 cm long, 4–5 mm thick. Seeds 1–1.5 mm long, 0.7–0.8 mm thick, ± obtusely angular, dark brown to black. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–May.

Type: Peru, Dep. Arequipa, Arequipa, 2,460 m, *R. S. Williams 2524* (NY).

Distribution (Fig. 226): Mountain slopes in the department of Arequipa, Peru, and the province of Tarapacá, Chile, 2,200–3,500 m elevation.

Specimens examined from cultivated plants:

PERU. AREQUIPA: Near Arequipa, road Chihuata/Puno, 2,700 m, *Santarius 2094, 2100*, 2101, 2114, 2119** (DUSS; *2100, 2119* also CTES, M; *2094, 2100* also MO).

Additional specimens examined:

PERU. AREQUIPA: Río Chile near Aequipa, ca. 2,530 m, *Munz 15538* (NY, POM, US). Quebrada de Lazaro, ca. 2,800 m, *Munz 15529* (NY, POM, US). Chachani mountains, *Hinck-*

ley 68 (GH, US). Morro Verde, 18 km above Yura, 2,870–3,000 m, *Straw 2351* (US, USM). Arequipa, 3,100–3,300 m, *Pennell 14279* (F). Characato, 2,600 m, *Vargas in 1949* (RSA). Chuquibamba near Condesuyos, ca. 3,200 m, *Stafford 1178* (K). Río Chile near Tingo, ca. 2,290 m, *Munz 15504* (F, G, GH, NY, POM, US). Arequipa, 2,300 m, *Günther & Buchtien 630* (HBG). Cachendo, 650 m, *Günther & Buchtien 2034* (HBG).

CHILE. TARAPACÁ: Pampa Ossa from Arica to La Paz, 2,200 m, *Ricardi 3438* (CONC). Pachica, *Ortega in 1880* (SGO). Libaya, *Rahmer in 1885* (SGO). Tarapacá, *Philippi* (CORD).

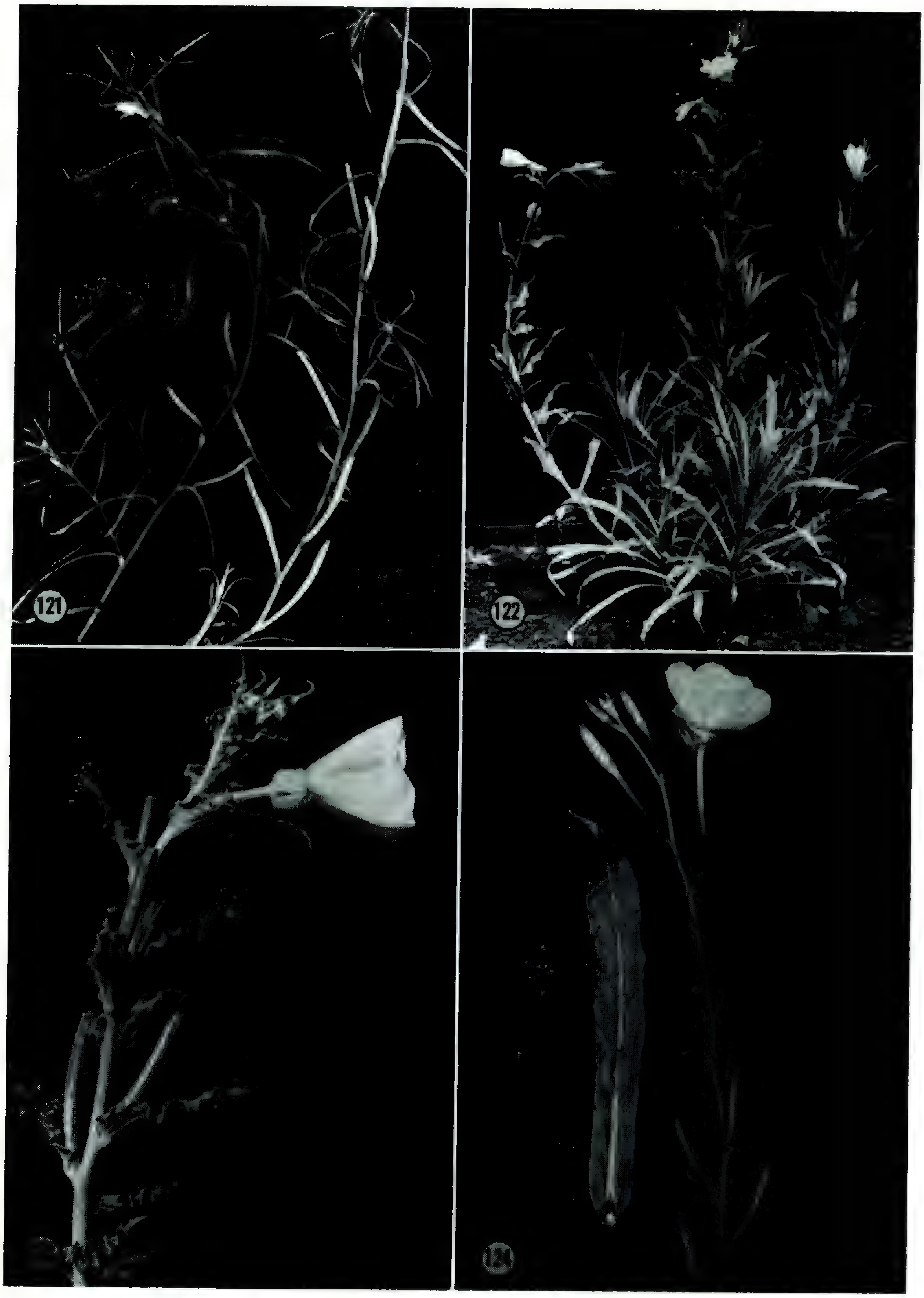
Oenothera rubida occurs with *O. peruana* and *O. verrucosa*. Although both of its chromosomal complexes are evidently derived from *O. peruana*, it is so clearly distinguished from that species by its more lax inflorescence, shorter capsules, and smaller flowers that it seems best to treat it as distinct. In addition, both genomes of the complex heterozygote *O. rubida* seem to include segments of the genomes of *O. scabra* and *O. verrucosa*, and so are not "pure" *peruana*. The inflorescence, which is often erect-villous, and the lack of a rosette, both seem to be indications of the influence of *O. scabra*, whereas the relatively slender capsule may be a result of the influence of *O. verrucosa*. Whether these influences represented hybridization between the species involved, or indicate that *O. rubida* originated before the full differentiation of the three other species under discussion from one another, is uncertain. One might assume, however, from the very limited range of *O. rubida* that it is a species of recent derivation, since there is no obvious reason why it could not spread as easily as the much more widely distributed *O. sandiana*. On the other hand, the complex heterozygosity of *O. rubida* seems to indicate that it is well established and that its persistence in nature is assured since hybrids with other entities have not been observed and are at the most very infrequent. This would tend to indicate a relatively great age, and the question must be left unsettled for the present.

10. **Oenothera tarijensis** Dietrich, sp. nov.—FIGS. 26, 116.

O. campylocalyx sensu Munz & Johnston, Contr. Gray Herb. 75: 22. 1925, pro parte.

Herba annua, non rosulata, ubique ramosa, 4–7 dm alta. Planta tota dense strigulosa, circum inflorescentiam pilis longis adpressis praedita. Folia caulina linearia vel angustissime elliptica, acuta, lamina in petiolum brevem gradatim decrescens, 7–20 cm longa, 1–1.5 cm lata; bractea anguste lanceolata, acuta, basi acuta vel rotundata, 4–7 cm longa, 0.5–1 cm lata; bractea sub anthesi maturitateque plerumque ad angulum 90° patentes; folia irregulariter obtuseque serrata. Inflorescentia simplex vel ramosa. Tubus floralis 3–5.5 cm longus. Gemmae ambito lanceolatae, 1–1.5 cm longae, 4–5 mm crassae, junctura sepalorum tubo florali anguste rubro-fasciatae; apices sepalorum divergentes, ca. 2 mm longi. Petala latissime obovata, lutea, saepe rubro basi et secus venos suffusa, 1.5–2 cm lata. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 9–13 mm longum. Capsula 2.5–3 cm longa, 5–7 mm crassa. Semina obtuse angulata, 1.3–1.5 mm longa, 0.9–1.1 mm lata, brunnea vel subnigra. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, branched throughout, 4–7 dm tall. Entire plant densely strigillose, with an admixture of appressed long-villous pubescence in the region of the inflorescence. Cauline leaves linear to very narrowly elliptic, acute, narrowed to a short petiole, 7–20 cm long, 1–1.5 cm wide; bracts narrowly lanceolate, acute, acute to rounded at the base, 4–7 cm long, 0.5–1 cm wide; bracts in flower and fruit mostly spreading at right angles; leaves usually plane at the margins and irregularly and bluntly serrate.



FIGURES 121–124. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia.*—121. *O. mendocinensis* (Argentina, Chubut, *Santarius 1354*).—122. *O. odorata* (Argentina, Río Negro, *Santarius 680*).—123. *O. odorata* (Argentina, Buenos Aires, *Santarius 329*).—124. *O. ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul, *Hackbart in 1966*).

Inflorescence simple or branched. Floral tube 3–5.5 cm long. Buds lanceolate in outline, red striped at the junction of the sepals with the floral tube, 1–1.5 cm long, 4–5 mm thick; apices of the sepals divergent, ca. 2 mm long. Petals very broadly obovate, yellow, often suffused with red at the base and along the veins, 1.5–2 cm long. Anthers 5–8 mm long. Filaments 10–14 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 4–6.5 cm long. Stigma lobes 3.5–6.5 mm long. Ovary 9–13 mm long. Capsule 2.5–3 cm long, 5–7 mm thick. Seeds 1.3–1.5 mm long, 0.9–1.1 mm thick, obtusely angular, dark brown to almost black. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: January–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 25 July 1972. Source: Bolivia, Dep. Tarija, between km 38 and 36 at the road from Villazón to Tarija, 3,200–3,300 m, 19 Mar. 1968, *K. A. Santarius 1924* (MO-2155393, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 227): Andes of Bolivia, 2,500–3,700 m elevation.

Specimens examined from cultivated plants:

BOLIVIA. TARIJA: At road from Villazón to Tarija, 38–30 km before Tarija, 2,900–3,300 m, *Santarius 1924**, *1949*, *1950**, *1955** (DUSS; 1955 also CTES; *1924*, *1955* also M; *1924*, *1949*, *1955* also MO).

Additional specimens examined:

BOLIVIA. LA PAZ: Vicinity of Sorata, 2,650–3,000 m, *Mandon 627* pro parte (W). Obrajes, 3,600 m, *Parodi 10152* (BAA, MO). La Paz, 3,550 m, *Buchtien 39* pro parte (US). TARIJA: Piños near Tarija, *Fiebrig 3358* (BM, GH, GOET, K, L, M, P, S). La Aguada near Villazón, *Balls 6120* (K, UC, US).

Oenothera tarijensis has one complex each from *O. versicolor* and *O. longituba*; the former (*Santarius 1946*) occurred with *O. tarijensis* at its type locality. The small leaves and flower color of *O. tarijensis* seem to be derived from *O. versicolor*, whereas the intermediate length of its floral tube can be attributed to *O. longituba*. Very likely the influence of *O. scabra* is also important in *O. tarijensis*, possibly through hybridization and partitioning of the genome, judging from the annual habit and lack of a rosette in both species, in contrast to the situation in *O. versicolor* and *O. longituba*.

11. **Oenothera recurva** Dietrich, sp. nov.—FIGS. 27, 117.

Herba annua erecta, non rosulata, omnino ramosa, 5–10 dm alta. Plantae dense strigulosae, ad basin glabescentes, circum inflorescentiam pilis longis erectis vel adpressis praeditae. Folia caulina anguste elliptica vel lanceolata ad anguste ovata, acuta, basi acuta vel truncata, sessilia vel breviter petiolata, 7–18 cm longa, (1–)1.5–2.5 cm lata; bractea lanceolata vel ovata, acuta, basi truncata, sessilia, 3–6 cm longa, 1–2 cm lata; bractea sub anthesi maturitateque plerumque sursum arcuata; folia irregulariter obtuseque serrata. Inflorescentia simplex vel ramosa, pro ratione laxa ut in *O. tarijense*, flore uno solo in diem aperiente. Tubus floralis (5–)6–9 cm longus. Gemmae ambito lanceolatae, saepe junctura sepalorum tubo florali rubrofasciatae, 1.5–2 cm longae, 5–6 mm crassae; apices sepalorum erecti, ca. 2 mm longi. Petala latissime obovata, lutea, raro rubro basi et secus venos suffusa, 2–3 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium ca. 10 mm longum. Capsula (1.5–)2–3 cm longa, 5–6 mm crassa. Semina 1.2–1.6 mm longa, 0.6–0.8 mm crassa, ± obtuse angulata, brunnea. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

FIGURE 125. *Oenothera ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul, *Hackbart in 1966*); *Oenothera* sect. *Oenothera* subsect. *Munzia*.

Erect annual herb, not forming a rosette, branched throughout, 5–10 dm tall. Plants densely strigillose, glabrescent near the base, with an admixture of erect or appressed long-villous pubescence in the region of the inflorescence. Cauline leaves narrowly elliptic or lanceolate to narrowly ovate, acute, acute to truncate at the base, sessile or short-petiolate, 7–18 cm long, (1–)1.5–2.5 cm wide; bracts lanceolate to ovate, acute, truncate at the base, sessile, 3–6 cm long, 1–2 cm wide; bracts in flower and fruit mostly curving upward; leaves undulate at the margins and irregularly and bluntly serrate. Inflorescence simple or branched, relatively lax as in *O. tarijensis*, with only a single flower opening each day. Floral tube (5–)6–9 cm long. Buds lanceolate in outline, often red striped at the junction of the sepals with the floral tube, 1.5–2 cm long, 5–6 mm thick; apices of the sepals erect, ca. 2 mm long. Petals very broadly obovate, yellow, rarely suffused with red at the base and along the veins, 2–3 cm long. Anthers 6–8 mm long. Filaments 10–17 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, (6–)7–10 cm long. Stigma lobes 5–7 mm long. Ovary ca. 10 mm long. Capsule (1.5–)2–3 cm long, 5–6 mm thick. Seeds 1.2–1.6 mm long, 0.6–0.8 mm thick, ± obtusely angled, dark brown. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: January–May.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 24 Sep. 1970. Source: Bolivia, Dep. Tarija, between km 32 and

30 at road from Villazón to Tarija, 2,900–3,000 m, 19 Mar. 1968, *K. A. Santarius 1952* (MO-2155699, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 228): Andes of Bolivia from La Paz to Tarija, 2,000–3,600 m elevation.

Specimens examined from cultivated plants:

BOLIVIA. TARIJA: At road from Villazón to Tarija, at km 35 and 32–30, 2,900–3,150 m, *Santarius 1941**, *1952** (DUSS, M, MO; *1941* also CTES).

Additional specimens examined:

BOLIVIA. LA PAZ: La Paz, 3,550 m, *Buchtien 39* pro parte (L, US). Obrajes, 3,550 m, *Buchtien 77* pro parte (K, L). COCHABAMBA: Colomí, Prov. Chaparé, 3,300 m, *Cárdenas 4257* (US). CHAPARÉ: Cerro de Chimoré, 2,300 m, *Troll 1179* (B).

Oenothera recurva has the *longituba*-complex in common with the very similar *O. tarijensis*. It can be distinguished from *O. tarijensis* principally by its broader leaves, longer floral tube, and erect villous pubescence in the inflorescence. Its second chromosomal complex is derived from *O. scabra*, which has very similar pubescence.

Since the chromosomally homozygous *O. versicolor* and *O. scabra* and the complex heterozygotes *O. tarijensis* and *O. recurva* often grow together, it is not surprising that hybrids should occasionally be formed. The progeny of *Santarius 1952* included a plant with a ring of 10 and a ring of 4 chromosomes, and it can only be interpreted as a spontaneous hybrid. As was emphasized in the introduction to this paper, such frequent hybridization suggests that the complex is in an active state of evolution at the present time.

12. **Oenothera sandiana** Hasskarl, Flora 33: 516. 1856; Retzia, Hort. Bogor. Descr. sive Retzia 1: 291. 1858.—FIGS. 118–119, 201–202.

O. weberbaueri Krause, Repert. Spec. Nov. Regni Veg. 1: 168. 1905. TYPE: Peru, Prov. Chicla, stony places along the railroad from Lima to Oroya, 3,720 m, 30 Dec. 1901, *A. Weberbauer 237* (B, destroyed in World War II; UC fragments and photograph, GH and POM photographs).

O. campylocalyx sensu Munz & Johnston, Contr. Gray Herb. 75: 22. 1925, pro parte.

O. campylocalyx sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 535. 1941, pro parte.

O. rubida sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 540. 1941, pro parte.

O. campylocalyx "Erlangen" Haustein, Z. Indukt. Abstammungs-Vererbungsl. 84: 418. 1952; Fischer, Feddes Repert. Spec. Nov. Regni Veg. 64: 237. 1962; Cleland, Jap. J. Genet. 43: 332. 1968.

O. campylocalyx sensu Munz, Opera Bot., Ser. B, 3: 39. 1974, pro parte.

Erect annual herb, not forming a rosette, unbranched or much branched in the lower portions, 3–10 dm tall. Plants densely to sparsely strigillose and also densely to sparsely covered with appressed or erect long-villous pubescence, always more heavily pubescent in the region of the inflorescence. Cauline leaves narrowly elliptic to lanceolate, acute, narrowly cuneate to truncate at the base, sessile or short-petiolate, 5–10 cm long, 1–3 cm wide; bracts lanceolate to narrowly ovate, acute, rounded to truncate at the base, sessile, 3–6(–8) cm long, 1–2.5 cm wide; all leaves plane to evidently undulate at the margins and regularly or irregularly but mostly bluntly serrate; bracts sometimes sinuate, with acute teeth. Inflorescence mostly unbranched, thicker than in *O. tarijensis* and *O. recurva*. Each day 1–3 new flowers opening; flowers sometimes exceeding

FIGURES 126–127. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia.*—126. *O. ravenii* subsp. *argentinae* (Argentina, Buenos Aires, *Santarius 342*).—127. *O. ravenii* subsp. *chilensis* (Chile, Cautín, *Stubbe in 1960*).

the apex of the stem by up to 2 cm. Floral tube 2–5.5 cm long. Buds oblong to narrowly ovate in outline, 1–2 cm long, 3–6 mm thick, usually red striped at the junction of the sepals with the floral tube; apices of the sepals erect or spreading, 1–2 mm long. Petals very broadly obovate, yellow, sometimes reddish at the base and along the veins, 1.5–2.5 cm long. Anthers 3.5–8 mm long. Filaments 7–10 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.5–6.5 cm long. Stigma lobes 3–6 mm long. Ovary 8–10 mm long. Capsule 1.5–2.5 cm long, 4–7 mm thick. Seeds elliptic to broadly elliptic in outline, brown to almost black, very rarely flecked with reddish brown. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14*, ring of 10 and 2 bivalents**, ring of 10 and ring of 4*** or ring of 12 and 1 bivalent**** at meiotic metaphase I). Flowering time: Ecuador and Peru, November–June; Bolivia, December–April.

Type: Cultivated at the Botanical Garden, Bogor, Java, Indonesia, 1855, *J. K. Hasskarl* (presumably at BO, not seen). Source: Peru, Dep. Puno, Sandia, east of Lake Titicaca, 1,500 m.

Distribution (Fig. 229): In the Andes from the department of Lambayeque, Peru to the department of Cochabamba, Bolivia, 2,000–4,000 m elevation, rarely lower. The stations in the provinces of Pinchincha, Latacunga, and Tunguragua in Ecuador, as well as in the province of Tarapacá, Chile, may represent introductions.

Specimens examined from cultivated plants:

ECUADOR. PICHINCHA: San Rafael, 3 km S of Quito, *Göpel in 1962** (DUSS, M, MO).

PERU. JUNÍN: Stony slopes at Río Mantaro, on both sides of the railway between km 296 and 298, 3 km SW of Jauja, 3,400 m, *Santarius 2125**, *2126**, *2127**, *2130*, *2133*, *2135*, *2139*, *2140**, *2142*, *2144*, *2152**, *2155*, *2158** (DUSS; *2127*, *2140*, *2152*, *2158* also CTES; *2126*, *2127*, *2140*, *2152*, *2158* also M; *2126*, *2127*, *2140*, *2142*, *2152*, *2158* also MO). AYACUCHO: Slopes, W edge of Ayacucho, 2,900 m, *Santarius 2206**, *2210*, *2212**, *2215*, *2218*, *2220*, *2224*, *2225*, *2230*, *2231*, *2233*, *2234* (DUSS; *2212* also CTES, M, SP; *2206*, *2212*, *2225*, *2234* also MO). Ucros, 116 km from Ayacucho on road to Andahuaylas, 3,150 m, *Santarius 2240**, *2241–2249*, *2250**, *2252–2255*, *2256**, *2257–2259*, *2260** (DUSS; *2240*, *2256*, *2260* also CTES; *2240*, *2250*, *2256* also M; *2240*, *2242*, *2248*, *2249*, *2250*, *2256*, *2260* also MO; *2250* also CTES, SP). CUZCO: Machu Picchu, 2,700 m, *Santarius 2266**, *2267*, *2268*, *2269**, *2270*, *2271* (DUSS; *2266* also MO); *Göpel in 1962** (DUSS, M, MO). Urubamba valley, along railway between Ollanta and Pachar at km 64.3, 2,750 m, *Santarius 2273****, *2274–2281*, *2283–2287*, *2289*, *2298–2295* (DUSS; *2273*, *2285* also MO). Urubamba valley, between Ollantaitambo and Pachar, at km 61.8, 2,800 m, *Santarius 2297****, *2298–2301*, *2304–2306* (DUSS; *2297* also CTES, M; *2297*, *2300* also MO). Urubamba valley, slopes S of Pisac, 3,050 m, *Santarius 2307**, *2308**, *2309**, *2310–2324* (DUSS; *2309* also CTES; *2308*, *2309* also M; *2307*, *2308*, *2309*, *2314*, *2317* also MO).

BOLIVIA. LA PAZ: Slope on east side of Valle de Irpaví, 0.5–1 km N of Calacoto, 3,450 m, *Santarius 2018**, *2021*, *2022**, *2023–2025* (DUSS; *2018* also CTES, M; *2018*, *2022*, *2023* also MO). COCHABAMBA: Ca. 26 km E of Cochabamba on road to Todos Santos, 2,900 m, *Santarius 1974**, *1976***, *1982*****, *1986* (DUSS; *1976* also CTES, M; *1976*, *1982* also MO), 32 km E of Cochabamba, 3,200 m, *Santarius 1992**, *1993*, *1994* (DUSS; *1992* also M, MO).

CULTIVATED: *O. campylocalyx* from the Botanical Garden in Erlangen, Germany, received 1960* (CTES, DUSS, M, MO).

Additional specimens examined:

ECUADOR. TUNGURAGUA: Between Pishilata and Ambato, 2,400–2,700 m, *Solis 9226* (F). COTOPAXI: Saquisili, 2,750 m, *Heiser 6067* (MO). LEÓN: Latacunga, 2,800 m, *Asplund 6929* (G, K, LD, S, US).

PERU. LAMBAYEQUE: Yanahuanca, ca. 3,050 m, *Macbride & Featherstone 1250* (F, GH, US). CAJAMARCA: La Herilla near Contumaza, *Sagasteguí et al. 6429* (US). LA LIBERTAD: Santiago de Chuco, Cachicadán, 3,050 m, *Lopez 449* (USM). Slopes above Yamobamba, ca. 70 km E of Trujillo, 3,000–3,100 m, *Conrad 2717*, *2755*, *2756*, *2757*, *2758*, *2760*, *2763* (MO). ANCASH: Baños de Chancos near Huaraz, ca. 2,750 m, *Sandeman 4618* (K). Ancash, *Raimondi* (USM). LIMA: Río Blanco, Prov. Huarochirí, 3,000–3,500 m, *Killip & Smith 21759* (NY, POM, US); *Macbride & Featherstone 721* (F, GH, US). Infiernillo near Huarochirí, 3,200 m, *Goodspeed et al. 11546* (GH, K, UC). Infiernillo, between San Mateo and Río Blanco, 3,300 m, *Ferreyra 8335* (BM, USM). Surco, 3,000–3,200 m, *Ferreyra 0666* (USM). Atsmita near Tupe, 3,100 m, *Cerrate 1059* (USM). JUNÍN: Prov. Tarma, Chuquishiunca near Huacapistama, between Tarma and San Ramón, 2,000–2,300 m, *Ferreyra 0437* (USM). Yanamayo between Palca and Acobamba, 2,600–2,700 m, *Ferreyra 3768* (US, USM). Hacienda San Juan near Jauja, 3,300 m, *Ferreyra 12918* (USM). Jauja, *Ridoutt 10783* (USM). Huancayo, 3,317 m, *Soukup 3574* (CORD, LIL, MO), *3163* (F); *Chávez 11932*, *12430* (USM); *Hoffmann 173* (M). PASCO: Between Salcachupán and Cerro de Pasco, 3,500–3,600 m, *Ferreyra 6601* (USM). HUANCAVELICA: Crocco near Conaica, 3,500–3,550 m, *Tovar 119* (US). Motca, 44 km SE Conaica, 3,400–3,450 m, *Tovar 260* (US). AYACUCHO: Aucará, *N.N. in 1967* (RSA). Apurimac, Abancay, 2,800–3,200 m, *Vargas 8994* (US). Andahuaylas, Chucheros, 3,000–3,200 m, *Riccio 243* (RSA). CUZCO: Urcos, 3,050–3,650 m, *Stafford in 1932* (K). Cerro Sacsahuamán, 3,400 m, *Ferreyra 2678* (USM). Chuspicanchis near Huarcapata, 3,100 m, *Vargas 1785* (GH). Ollantaytambo, *Munz 15543* (POM). 2,900 m, *Herrera 689* (F, US). Urubamba valley, between Yuncapate and Sta. Rita, 2,800 m, *Vargas 2697* (MO). Hacienda Sta. Rita, *Dreyfus 12789* (USM). Puente Urubamba, 2,810 m, *Vargas 7886* (LIL). Paucartambo valley, 3,000 m, *Vargas 671* (MO); 3,300 m, *Woytkowski 228* (USM); *Herrera 3359* (F, POM). Road to Pillahuata, km 79, 2,900 m, *Ugent & Vargas 4415* (K); 2,800 m, *Woytkowski 68* (USM). Hacienda Phuycella, 3,400 m, *Herrera 2979* (US). Alcumbrera near Chateca, 3,450 m, *Herrera 1090* (BM, F, GH, K, MO, US). Machu Picchu, 2,400 m, *Herrera 1989* (F); 2,600 m, *Munz 15546* (POM); ca. 2,130 m, *Sandeman 3,640* (K); *Tutin 1293* (BM). Vicinity of Cuzco, 3,500 m, *Herrera 3* (LIL); 3,000-3,600 m, *Herrera in 1923* (GH, US); *Herrera 3051* (US); *Rose 19065* (US); 3,660 m, *Munz 15541* (NY, POM, US). Pisac near Calca, 3,000 m, *Marin*

25 (F, LIL); *Juzepczuk 10780* (LE). Vitcabamba near Calca, 2,100–2,700 m, *Vargas 3822* (MO). Haciendo Orco near Calca, *Hammarland 588* (S). PUNO: Prov. Carabaya, road between Ollachea and Farina, *Raimondi in 1864* (USM). Ollachea, 2,500 m, *Vargas 6940* (POM). Isla de la Laguna de Titicaca, *Raimondi in 1864* (USM). Road from Puno to Juliaca, 3,800 m, *Ugent 5246* (K). Quicacha, *Raimondi 187* (USM).

BOLIVIA. LA PAZ: Prov. Nor Yungas, Chirca, 2,500 m, *Eyerdam 25352* (F, GH, K, MO, US). La Paz, 3,600 m, *Parodi 10152* (POM); 3,500 m, *Shepard 217* (GH, POM, UC, US); COCHABAMBA: Chaparé, road to Chimoré, 32 km NE Cochabamba, 1,200 m, *Eyerdam 24996* (F, K, UC). Ansalso, between Cochabamba and Vilavila, 2,600 m, *Eyerdam 25078* (F, GH, K, UC).

CHILE. TARAPACÁ: Mamiña, 2,700 m, *Ricardi 4700-1085* (CONC).

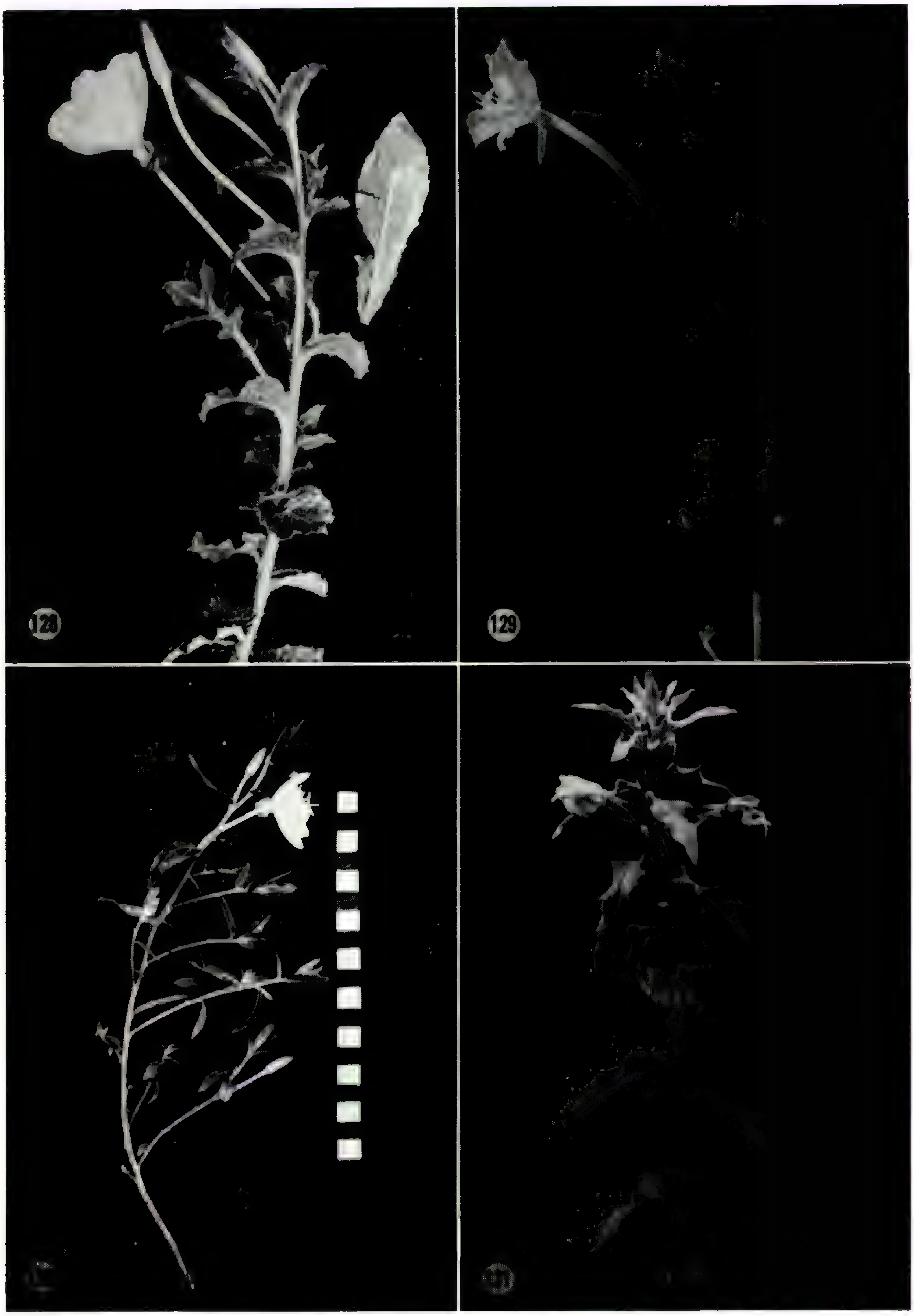
Since no fewer than four different chromosomal complexes are involved in the origin of *O. sandiana*—those from *O. peruana*, *O. versicolor*, *O. longituba*, and *O. scabra*—it is not surprising that it includes a wide array of different forms. The major role is, however, played by *O. versicolor* and *O. scabra*. It has not proven possible to divide this species into useful infraspecific categories, however.

Even the variation in single populations is astounding at times. Growing next to plants which are more or less intermediate between *O. versicolor* and *O. scabra* occur others which resemble one or the other species more strongly. In addition to these, there occur plants which clearly show characteristics of *O. longituba*, such as a long floral tube and flowers that overtop the shoot apex. At other places, principally in the Bolivian portion of the range, the influence of *O. longituba* is noticeably stronger. It can be assumed that the genomes of this north-Argentinian species has introgressed into *O. sandiana* by way of *O. tarijensis* and *O. recurva*, or even by *O. elongata* and *O. pseudoelongata* (series *Clelandia*), and that in passing northward the influence of the *longituba*-complex becomes less and less.

The chromosomal complexes that occur in *O. sandiana* seem rarely to occur in unaltered form, and evidently mechanisms have operated to intermix the genomes of the species involved in its origin. It seems clear that whatever the pairing relationships of the chromosomes in the complex heterozygote that the genes determining the major phenotypic characteristics have to some extent been substituted for in the course of evolution. Moreover, additional reciprocal translocations between nonhomologous chromosomes could lead to a breaking-up of the ring of 14 and the origin of unstable chromosomal complexes.

Since *O. versicolor* and *O. scabra* are chromosomally homozygous throughout the entire range of *O. sandiana*, it seems logical to assume occasional backcrossing between the complex heterozygous derivative and its parents, the plants involved being more or less typical of the species or perhaps already altered by hybridization themselves. This would inevitably lead to the production of plants that are not strictly intermediate between *O. versicolor* and *O. scabra*. Between a complex heterozygote and the species that participated in its formation there are usually no barriers to hybridization or recombination.

Within the very different appearing individuals of this species spontaneous hybrids with small rings of chromosomes or bivalents arise infrequently. From this it may be concluded that among the variety of end arrangements that presumably exist in at least many populations of the species, there is a sort of



FIGURES 128–131. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—128. *O. longiflora* subsp. *grandiflora* (Argentina, Corrientes, *Krapovickas & Cristóbal 11293*).—129. *O. longiflora* subsp. *longiflora* (Uruguay, Colonia, *Santarius 73*).—130. *O. catharinensis* (Brazil, Santa Catarina, *Conrad & Dietrich 13*).—131. *O. indecora* subsp. *indecora* (Uruguay, Florida, *Santarius 206*).

equality or balance between them so that hybrids always have a ring of 14 chromosomes, even though it may be formed in various ways and through the association of various combinations of chromosome ends. If this equality of genomes is disturbed, apparently there is a selection for end arrangements that will lead predictably to the consistent formation of plants with a ring of 14 within the population.

13. **Oenothera nana** Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 143. 1874. —Figs. 1, 24, 120, 203–204.

O. punae sensu Munz & Johnston, Contr. Gray Herb. 75: 19. 1925, pro parte.

Annual to perhaps perennial plants, growing only as a rosette, but often with a central shoot up to 10 cm long and short, prostrate side branches. Plants either exclusively and densely strigillose or, especially in the inflorescence, with an admixture of appressed long-villous pubescence. Leaves linear to very narrowly elliptic, acute, the lower ones gradually narrowed to the petiole, the upper ones ± sessile, narrowly cuneate to acute at the base; leaves plane or ± undulate at the margins, irregularly serrate with blunt or acute teeth, often flecked with dark brown or black. Flowers formed in the axils of the rosette leaves. Floral tube 4–10(–15) mm long. Buds oblong to broadly oblong or broadly elliptic to rotund in outline, green to yellowish, often flushed with red, 2–4 mm long, 2–3 mm thick; apices of the sepals ca. 0.5 mm long, erect or divergent. Petals very broadly obovate, rounded or retuse, yellow, often flushed with red, 3–5 mm long. Anthers 2–3 mm long. Filaments 3–4 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 6–13 mm long. Stigma lobes 1.5–2 mm long. Ovary 5–10 mm long. Capsule narrowly lanceolate to lanceolate in outline, 1–2 cm long, 3–4 mm thick, standing at right angles to the stem, often arched downward at the apex. Seeds 0.7–1.1(–1.5) mm long, 0.4–0.5(–0.8) mm thick, broadly elliptic to rotund, rarely obtusely angled, light to dark brown, often with darker flecks. Self-pollinating; complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: Peru, Chile, and Bolivia, December–April; Argentina, December–March.

Type: Argentina, Prov. Catamarca, sandy alpine valleys between Nacimientos and Laguna Blanca, end of Jan. 1870, *P. G. Lorentz 467* (GOET, holotype; CORD, isotype).

Distribution (Fig. 232): Andes from the departments of Puno and Arequipa in Peru, just touching northernmost Chile, and through Bolivia to the province of San Juan in Argentina, 2,500–4,700 m elevation.

Specimens examined from cultivated plants:

PERU. PUNO: Sandy places 2 km SE of Zepita, 3,820 m, *Santarius 2035, 2036*, 2037–2039* (DUSS; *2039* also CTES, M; *2035, 2038, 2039* also MO). Sandy slopes above Chimu, 8 km SE of Puno on road to Chucuito, 3,900 m, *Santarius 2045* (CTES, DUSS, M, MO); 4,000 m, *Santarius 2046* pro parte, *2049–2053, 2055** pro parte, *2056*, 2058** (DUSS; 2051, 2055 also CTES; *2046, 2051, 2055, 2056, 2058* also M, MO).

BOLIVIA. POTOSÍ: Waste places in E part of Potosí, 4,100 m, *Santarius 1961, 1966–1969* (DUSS; *1966* also CTES, M, MO).

ARGENTINA. JUJUY: Puna vegetation, 1 km S of Abra Pampa, *Santarius 1886** pro parte (DUSS, M, MO). Sandy places in puna vegetation, 3 km E of La Quiaca on road to Yavi, 3,550 m, *Santarius 1888*, 1889, 1890, 1892–1897, 1899, 1900–1904, 1905*, 1906–1908* (DUSS; *1895, 1905* also CTES, M; *1888, 1895, 1897, 1905* also MO). Sandy places 4 km W of Yavi, 3,600 m, *Santarius 1910*, 1911, 1912, 1914–1922* (DUSS; *1910* also CTES, M; *1910, 1916* also MO). CATAMARCA: Sierra de Ambato, top of Cerro Manchado, 4,300–4,450 m, *Hunziker 72-1345** (DUSS, MO).

Additional specimens examined:

PERU. AREQUIPA: Chiguate, 2,700 m, *N.N. in 1954* (RSA). MOQUEGUA: Carumas near Volcán Ticsaní, 4,000 m, *Weberbauer 7324* (F, GH, POM, S, US). PUNO: Sta. Lucia near Puno, ca. 4,700 m, *Sharpe 137* (K). Between Ilave and Mazo Cruz, 3,850 m, *Tovar 5294* (USM). Occa Pampa near Huancané, ca. 3,800 m, *Shepard 86* (GH). Vilque, 3,750 m, *Iltis & Ugent 1354* (K).

CHILE. TARAPACÁ: Putre near Arica, 4,000 m, *N.N. in 1948* (K). Caritaya near Tranque, 3,600 m, *Behn 19602* (CONC).

BOLIVIA. LA PAZ: 3,900 m, *Buchtien 644* (NY, US), *644a* pro parte (US), 3,700 m, *Buchtien 654* (GH, NY). Guaqui, 3,900 m, *Asplund 5983* (US). Guayamarca near Caño, *D'Orbigny 1930* (P). Pacajes, Ulloma, 3,800 m, *Asplund 4467* (UPS). Near Corocoro, 4,200 m, *Asplund 4467* (UPS). COCHABAMBA: Cona Cona station on the line from Oruro to Cochabamba, ca. 3,960 m, *Brooke 5214* pro parte (BM). Potosí, Uyuni, 3,700 m, *Asplund in 1921* (US). TARIJA: Between Quebrada and Salitre, ca. 4,000 m, *Fries 1028* (S).

ARGENTINA. JUJUY: Tumbaya, Abra de Pibes, 4,000–4,050 m, *Sleumer 3274* (LIL). Humahuaca, Tres Cruces, 3,700 m, *Cabrera et al. 15243* pro parte (LP); *Venturi 10088* (US). Dep. Cochinoca, Laguna Tres Cruces, 3,700 m, *Claren 11678* (CORD). Humahuaca, Cerro La Soldad, 3,500 m, *Venturi 9010* (US). Sta. Catalina, 3,400–4,300 m, *Kurtz 11454* (CORD, POM); 3,650 m, *Claren in 1901* (S). Dep. Tilcara, Yala de Monte Carmelo, 2,900 m, *Fabris 6402* (BAA, MO). Moreno, 3,500 m, *Fries 938* (S). Yaví, 3,600 m, *Sleumer 3603* (LIL); 3,500 m, *Fries 938a* (S); *Cabrera 21470* (LP). Susques, 3,700 m, *Cabrera 8750* (LP); *Castellanos in 1927* (POM). Sierra de Aguilar, Vicuñayua, 3,900 m, *Schwabe 514* (BAB). Citeara, 3,000 m, *Venturi 6512* (US). SALTA: El Alisal, 2,800 m, *Rodríguez 1292* (LIL, POM). La Laguna, Cerro Cajón, 3,900 m, *Rodríguez 1292* (SI). Montañas, *Rodríguez 1525* (BA). San Carlos, Cerro de Cachi, 4,400 m, *Venturi 6948* (US). TUCUMÁN: Cerro Muñoz near Tafí, *Fabris 1517* (LP); 4,000 m, *Lillo 4188* (GH, LIL, POM), 3,900 m, *4223, 7409* (LIL). Peak of Calchaquies, 4,200 m, *Lillo 5516* (LIL, MO, POM). Tafí, Infiernillo, *Castillon 3185* (LIL). Tafí, Las Lagunas, 4,000 m, *N.N. in 1926* (LIL 80079). Cerro Negrito, 4,100 m, *Sparre 6121* (LIL), 4,100 m, *6059* (LIL), 4,300 m, *8610* (LIL). Peak of Chaquivil, *Olea 248* (NY). Distr. Cabalao del Valle, Cajón, 3,900 m, *Schretter 4791* (LIL). CATAMARCA: Cerro Yutuyaco, 3,600–3,800 m, *Sleumer 2724* (LIL). Río Potrero near Choyana, 3,600 m, *Sleumer 1926* (LIL). Tinogasta, 3,100 m, *Schmitz 6251* (LIL). From La Coipita to Vallecito near Tinogasta, 3,100 m, *Schreiter 6251* (LIL). Sierra de Ambato, Cerro Manchado, 4,300–4,450 m, *Hunziker 20853* (CORD), 3,500 m, *20983* (CORD), 4,000–4,100 m, *20010* (CORD), 3,300–3,400 m, *Hunziker 19766* (CORD). LA RIOJA: Sierra de Famatima, Vega del Real Viejo, *Kurtz 14780* (CORD). SAN JUAN: Cerro Tronador, Cuesta Las Casitas, *Spegazzini 212* pro parte (BAB).

The species, which has been known for a long time in the literature and in the herbarium as *O. nana*, *O. punae*, or *O. kuntziana*, is made up of two different elements. To the first belong plants with two chromosomal complexes from series *Renneria*, and this group includes the type of *O. nana*. To the second group belong plants in which are combined one genome from series *Renneria* and one from series *Allochroa*. These plants belong by definition to subsect. *Clelandia*. For them, the name *O. punae* is to be used.

It is clear that the complex heterozygous *O. nana*, with its very condensed habit, has been derived from plants of normal stature in the process of adaptation to the extreme conditions at the high elevations where it occurs. I have already referred to *O. lasiocarpa* as a transitional species, and there are plants in *O. nana* which have some of the characteristics of that species.

On account of the extremely condensed habit of *O. nana*, a complex mode of adaptation that alters the expression of many characteristics, it is difficult to analyze the origin of this species. The analysis of hybrids with species of normal stature has revealed, however, the probable influence of *O. peruana*, *O. versicolor*, *O. lasiocarpa*, and *O. scabra* each with varying expression of their features in *O. nana*. The influence of *O. versicolor* and *O. lasiocarpa* appears to be stronger in the southern part of the range of *O. nana*, and that of *O. peruana* and *O. scabra* seems stronger in the north.

The individuals in a population are rarely uniform, but vary in the same way as has been discussed for *O. sandiana*. The situation is made still more complex by the fact that *O. nana* occurs together with *O. punae* at many localities, and their chromosomal complexes are essentially interchangeable with one another; see also the remarks on p. 611 in this connection.

The nanism of *O. nana*, its most prominent characteristic, can be manifested in various ways. Both complexes can have the dominant traits for normal size expressed, or one complex can be dominant and the other intermediate or recessive.

Series II. ALLOCHROA

Oenothera sect. **Oenothera** subsect. **Munzia** series **Allochroa** (Fischer & Meyer) Dietrich, comb. nov. Based on *Oenothera* sect. *Allochroa* Fischer & Meyer, Ind. Sem. Hort. Petrop. 2: 44. 1836.

Onagra sensu Moench, Meth. Pl. 1: 675. 1794, pro parte; Suppl. Meth. Pl. 2: 287. 1802, pro parte.
Oenothera sect. *Onagra* Séringe ex DC., Prodr. 4: 46. 1828, pro parte.
Oenothera sensu Spach, Nouv. Ann. Mus. Hist. Nat. 341. 1835, pro parte.
Oenothera sensu Raimann, in Engler & Prantl, Nat. Pflanzenfam. III, 7: 214. 1893, pro parte.
Raimannia sensu Sprague & Riley, Bull. Misc. Infor. 1921: 200. 1921, pro parte.
Oenothera § *Raimannia* sensu Munz & Johnston, Contr. Gray Herb. 75: 16. 1925, pro parte.
Oenothera subgen. *Raimannia* Munz, Physis 11: 279. 1933, pro parte; Amer. J. Bot. 22: 645. 1935, pro parte; Revista Univ. (Santiago) 22: 261. 1937, pro parte; Comun. Bot. Mus. Hist. Nat. Montevideo 1(10): 26. 1943.
Oenothera subgen. *Raimannia* sect. *Raimannia* Munz, North Amer. Fl., ser. 2, 5: 105. 1965, pro parte.

Erect annual or biennial herbs, rarely prostrate, forming a rosette or the stem elongating soon after the development of a few basal leaves, unbranched or with a branched main stem and ascending branches from the rosette which either arch outward in ascending or rise sharply and abruptly; plants 0.5–15 dm tall, rarely even taller. Stems more slender than in series *Renneria*, 2 to at most 10 mm thick. Plants (1) exclusively strigillose; (2) densely to sparsely strigillose, densely to sparsely long- and short-villous, the hairs mostly appressed, and densely to sparsely glandular-pubescent; (3) very densely to sparsely long- and short-villous and densely to sparsely glandular-pubescent; or (4) densely short-villous and densely glandular-pubescent. Rosette leaves linear to oblong, very narrowly oblanceolate to oblanceolate or narrowly elliptic, long- or short-acute, sessile and narrowly cuneate to truncate at the base or gradually narrowed to the petiole, 8–25 cm long, 0.4–3.5 cm wide; cauline leaves linear to oblong, very

narrowly elliptic to elliptic or narrowly lanceolate to narrowly ovate, acute, sessile, narrowly cuneate to truncate at the base, 2–20 cm long, 0.2–3 cm wide; bracts linear to broadly oblong, narrowly elliptic to elliptic or narrowly lanceolate to ovate, acute to obtuse, rarely almost rounded, sessile, acute to subcordate at the base, 2–10 cm long, 0.2–2.5 cm wide; leaves mostly irregularly and distantly serrate with dull teeth, occasionally very coarsely serrate or doubly serrate (*O. coquimbensis*), plane or evidently to very slightly undulate along the edges. Inflorescence unbranched or branched, lax; flowers erect in anthesis, one opening each day. Floral tube 0.5–13 cm long. Buds oblong, elliptic to broadly elliptic or narrowly lanceolate to narrowly ovate in outline, 0.3–3.5 cm long, 2–11 mm thick, often with red stripes at the junction with the floral tube. Sepals green or yellowish green, often flushed with red, sometimes densely to sparsely flecked with dark red; apices of the sepals 0.5–4 mm long, erect, spreading, or hornlike. Petals obovate to very broadly obovate, rarely elliptic to broadly elliptic, rounded or retuse, 0.3–5 cm long, yellow to bright yellow, sometimes with a red basal spot. Ovary 1–2.5 cm long. Capsule linear to narrowly oblong in outline, terete, rarely slightly enlarged in the upper third or tapering at both ends and appearing short-petiolate, projecting obliquely from the stem, straight or slightly curved, (1.5–)2–6 cm long, 2–5 mm thick, not fused with the bract; valves curving outward or inward after the capsule dehisces, occasionally spreading. Seeds 1–2 mm long, 0.4–1.1 mm thick, narrowly elliptic to rotund in outline, light or dark brown to almost black. Self-compatible; chromosomal homozygotes or self-pollinating complex heterozygotes, rarely outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents, ring of 14 or intermediate configurations at meiotic metaphase I).

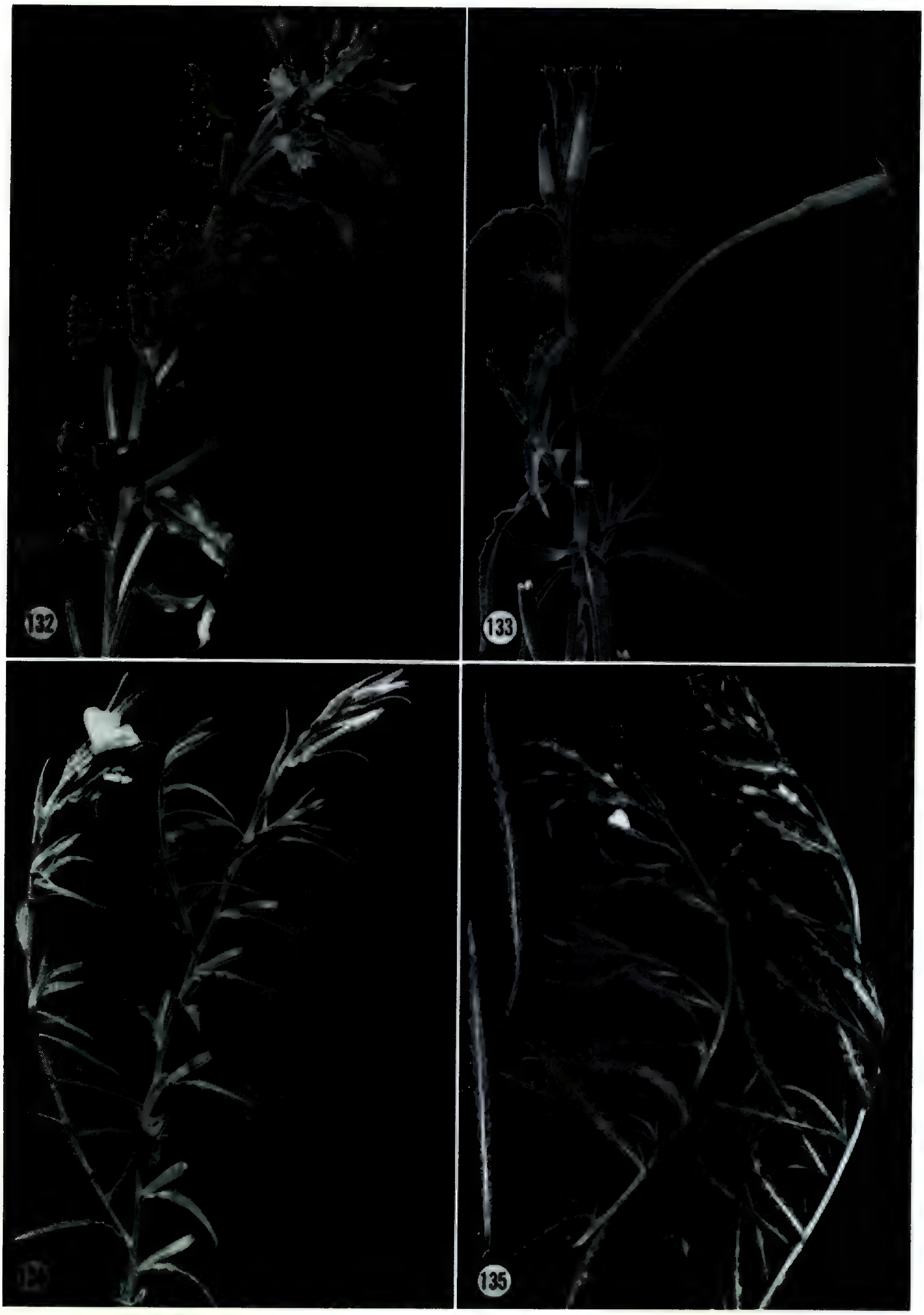
Type species: *Oenothera mollissima* L.

Distribution (Fig. 7): These are predominantly plants of relatively low elevations from sea level upward; ascending to 3,200 m elevation in the Andes (*O. affinis*, *O. arequipensis*, *O. featherstonei*, *O. nocturna*, *O. odorata*, *O. verrucosa*). In Brazil, the plants occur in Guanabara, southern Minas Geraís, and in São Paulo to Rio Grande do Sul. They occur throughout Uruguay and in all provinces of Argentina as far as Río Gallegos in Patagonia, extending northward to Tarija in Bolivia. West of the Andes, they range in Chile from the provinces of Atacama to Magellanes, and in the coastal deserts and semideserts from the department of La Libertad in Peru to Valparaíso in northern Chile. In Peru they ascend into the mountains along river valleys to 3,200 m elevation.

If the isolated stations that occur up to 3,200 m elevation in the Andes are disregarded, most species of this series are inhabitants of the broad plains of Argentina and the coastal regions on both the Atlantic and Pacific shores of southern South America, and the lowermost slopes of the mountains.

All species have more slender stems and are more graceful than the sturdy, thick-stemmed species of series *Renneria*. Important differences from that series are the laxer inflorescences, erect flowers, and obliquely divergent capsules.

Most of the species of series *Allochroa* form a rosette, like the majority of those of series *Renneria*. Among the chromosomally homozygous species, only



FIGURES 132–135. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—132. *O. indecora* subsp. *bonariensis* (Argentina, Buenos Aires, *Santarius 278*).—133. *O. affinis* (Argentina, Tucumán, *Santarius 1801*).—134. *O. mollissima* (Uruguay, Montevideo, *Santarius 42*).—135. *O. rivadaviae* (Argentina, Chubut, *Santarius 924*).

O. affinis, *O. catharinensis*, *O. coquimbensis*, and *O. verrucosa* form no rosette; whereas among the complex heterozygotes, no rosette is formed by those which incorporate a genome from *O. affinis*: namely, *O. mollissima*, *O. montevidensis*, and *O. picensis*.

14. **Oenothera mendocinensis** Gillies ex Hooker & Arnott, Bot. Misc. 3: 310. 1833.—FIGS. 35–36, 121, 174, 210.

O. odorata sensu Hicken, Physis 2: 110. 1916.
Raimannia mendocinensis (Gillies ex Hooker & Arnott) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.
Oenothera argentinae H. Lév. & Thell. var. *camptotricha* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherlands, Rotterdam, Maashaven meal factory, 10 Sep. 1920, *A. W. Kloos* (BAS).
O. indecora sensu Munz, Physis 11: 281. 1933, pro parte; Amer. J. Bot. 22: 658. 1935, pro parte.

Erect annual herb, forming a rosette, unbranched or with a branched main stem and widely arching or obliquely ascending side branches arising from the rosette, 3–6 dm tall. Plants either exclusively and densely strigillose or densely to sparely strigillose and densely to sparely villous, but often strigillose only near the base. Rosette leaves linear, acute, narrowed to the petiole, 7–14 cm long, 3–5 mm wide; cauline leaves linear, acute, 3–6 cm long, 2–4 mm wide; bracts linear, acute, truncate at the base, sessile, 3–5 cm long, 1–3 mm wide, mostly somewhat longer than the capsules or ± the same length; leaves plane or slightly undulate at the margins, irregularly serrate. Inflorescence branched. Floral tube 0.5–1.5 cm long. Buds oblong to elliptic in outline, gray green, often flushed with red, 4–9 mm long, 2–4 mm thick; apices of the sepals erect, 0.5–1 mm long. Petals very broadly obovate, 0.5–1 cm long. Anthers 2.5–5 mm long. Filaments 3–5 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 8–21 mm long. Stigma lobes 2–3.5 mm long. Ovary 1.2–1.8 cm long. Capsule (2–)3–6 cm long, 2–3 mm thick. Seeds elliptic in outline, light brown, (1–)1.2–1.8 mm long, 0.5–0.7 mm thick. Self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: October–March.

Lectotype: Argentina, Prov. Mendoza, between Las Chacayes and Melocotón, foot of the Andes of Mendoza, (1824?), *Gillies* (K, POM photograph; a photograph of isolectotype at E, from Herb. GL). Two sheets of the type collection are in K, both mixed with *O. indecora* (one collected by Charles Darwin at Bahía Blanca in 1832). Because *O. indecora* does not occur in the province of Mendoza and because it cannot be determined with certainty which plants the labels correspond to, only one branch has been selected as lectotype. For this branch, the correspondence of the plant with the label is clear.

Distribution (Fig. 226): Occurs only at low elevations, ascending to 1,500 m in the Andean foothills of Mendoza. The range includes the following provinces of Argentina: Mendoza, San Luis, Córdoba, Buenos Aires, La Pampa, Río Negro, Chubut, and Santa Cruz.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Dunes ca. 2 km SE of Argerich, 37 km W of Bahía Blanca, *Santarius 402*, 411*, 412, 415*, 417, 420*, 421*, 423, 425, 431*, 433, 435*, 438, 442*, 443, 445, 448* (DUSS; *402, 420, 421* also CTES; *402, 415, 420, 421, 442* also M; *402, 420, 421, 425* also MO). Dunes along road from Villa del Mar to Ruta 229, ca. 5 km NNW of Punta Alta, *Santarius 518*, 521, 529, 533*, 536* (DUSS; *533* also M; *521, 533* also MO). CHUBUT: Dunes SE of Puerto Madryn, *Santarius 1354*, 1356*, 1358, 1361, 1367, 1371, 1374*, 1378, 1382, 1390* (DUSS; *1354, 1374* also CTES; *1354, 1356, 1374* also M; *1354, 1371, 1374* also MO).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: Daireaux, *Parodi 13163* (BAA). Monte Veloz, *Parodi 12238* (BAA). General Villegas, dunes near Bunge, *Cabrera 5703* (LP). Between Piedritas and Cañada Seca near General Villegas, *Hunziker 12826* (CORD, MO). Salliquelo, Est. "Los Gorros" near Pellegrini, *Cabrera 8012*, (F, GH). Dunes near Pellegrini, *Cabrera 6955* (LP). Punta Alta, *O'Donell 1513* (LIL). Colonel Dorrego, Monte Hermoso, *Erettowi 2607* (MO). From Urdampilleta to Piravano on Ruta 205 near Bolívar, *Vervoorst 5437* (BAB). 25 km SE Carmen de Patagones, *Fabris & Schwabe 5001* (LP). Río Negro near Carmen de Patagones, *Hunziker 414* (CORD); *Meyer 6991* (LIL). Between Bahía San Blas and San Blas, *Ameghino in 1903* (POM). Villarino near Bahía Blanca, *Correa 2387* (BAB); *Boelcke 11788* (BAA, MO, SI). Ruta 22, *Puerto 11552* (MVFA). Argerich near Villarino, *Parodi 13799* (BAA, MO). Agustina near Junín, *Cabrera 6560* (F, SP, NY). CÓRDOBA: Near Pacheco de Melo, road to Laboulaye, *Hunziker 12768* (CORD, MO), *12779* (CORD). Between Laboulaye and Salguero, *Hunziker 12810* (CORD, MO, RSA). Sierra Chica, La Redución, *Burkart 17325* (SI). Laguna Brava, 400 m, *King 319* (BM). Quinta Soriano N of Bajo Grande near Córdoba, *Kurtz 16128* (CORD, MO). Between Est. S. Miguel and Rufino near Santa Fé, *Spegazzini 6915* pro parte (BAB). Between Rufino and La Cesira, *Hunziker 12853* (RSA). Sierra Ochoa, *Stuckert 13562* (G). Dep. Unión, La Carlota, *Hunziker 11206* (CORD, MO). Est. La Mascota near Ballesteros, *Hunziker 12751* (CORD, RSA). SAN LUIS: Laguna near Sayape, *Castellanos in 1949* (LIL). Pedernera on Ruta 148, 10 km S Villa Mercedes, 510 m, *Anderson 1338* (LP). Villa Mercedes, *Corradi 4832* (SI). Between Villa Mercedes and Juan Jorba on Ruta 8, *Hunziker 13170* (CORD, RSA). Near Esquina on Ruta 7, between San Luis and E. Lobos, *Hunziker 13123* (CORD). Dep. General Pederrera, on Ruta 148 between Laraisse and El Durazno, 500 m, *Hunziker 15977* (CORD). Nueva Escocia, *Burkart 10840, 10808* (LIL, SI). LA PAMPA: Guatraché, *Viguier 94* (BAB). General Pico, *Burkart 9919* (LIL, SI). General Acha, *Orbea in 1953* (SI, US); *Burkart 19205* (SI). Between General Acha and Santa Rosa, *Troncoso in 1959* (SI). General Lagos (SI-4856). Laguna La Asturiana, *Bacigalupo in 1959* (P, SI). La Pampa, *Monticelli 39* (SI). MENDOZA: Las Heras, La Crucesita, *Ruiz Leal 5378* (Leal). Mina Atalu, *Ruiz Leal 3328* (Leal). Dep. Tunuyán, La Piedra Rajada, *Ruiz Leal 1707* (Leal). Tupungato, road to Est. Silva, 1,500 m, *Cáceres 6* (LIL, NY). 10 km W Campo de Los Andes, 1,500 m, *Araque & Barkley 20Mz179* (LIL). Tupungato, *Ruiz Leal 2784a* (LIL). Dep. San Carlos, Est. Viluco, *Torres 36* (SI). Mendoza, *Jörgensen 131* (BAB, C). RÍO NEGRO: S. Antonio, *Guernant in 1910* (LIL). General Roca, 250–360 m, *Fischer 86* (BM, F, GH, K, MO, NY, SI, US). Dep. General Roca, banks of Río Negro near J. J. Gomez, *Krapovickas et al.* (CTES). Río Negro, *Berg 98* (CORD); *N. N. 88 in 1874* (LE). SANTA CRUZ: Territory of Santa Cruz, *Ameghino 32* (BA).

Specimens from outside of South America:

NETHERLANDS. Rotterdam, 1902, *Jansen & Wachter 13286* (L); 1931, *Kern & Reichgelt 12181* (L).

GERMANY. Emmerich on Rhine River, 1931, *Kern & Reichgelt 5064* (L).

Its small flowers, very small leaves, mostly long and narrow fruits, and strigillose pubescence set off *O. mendocinensis* as an isolated species. On the basis of the pubescence, it might be regarded as the least specialized species of the series, since it is the only chromosomally homozygous member of series *Allochroa* which has retained this characteristic of the members of series *Renneria*. On account of its slender habit and small flowers, *O. mendocinensis* has been included incorrectly in the synonymy of *O. indecora*, on the assumption that a marked similarity between these species indicates a close relationship. The hybrid between *Santarius 405* (*O. mendocinensis*) and *O. argentinae "Erlangen"*

(= *O. indecora* subsp. *bonariensis*) formed 7 bivalents at meiotic metaphase I, from which it cannot be inferred, however, that *O. mendocinensis* and *O. indecora* are closely related, as discussed in the introduction.

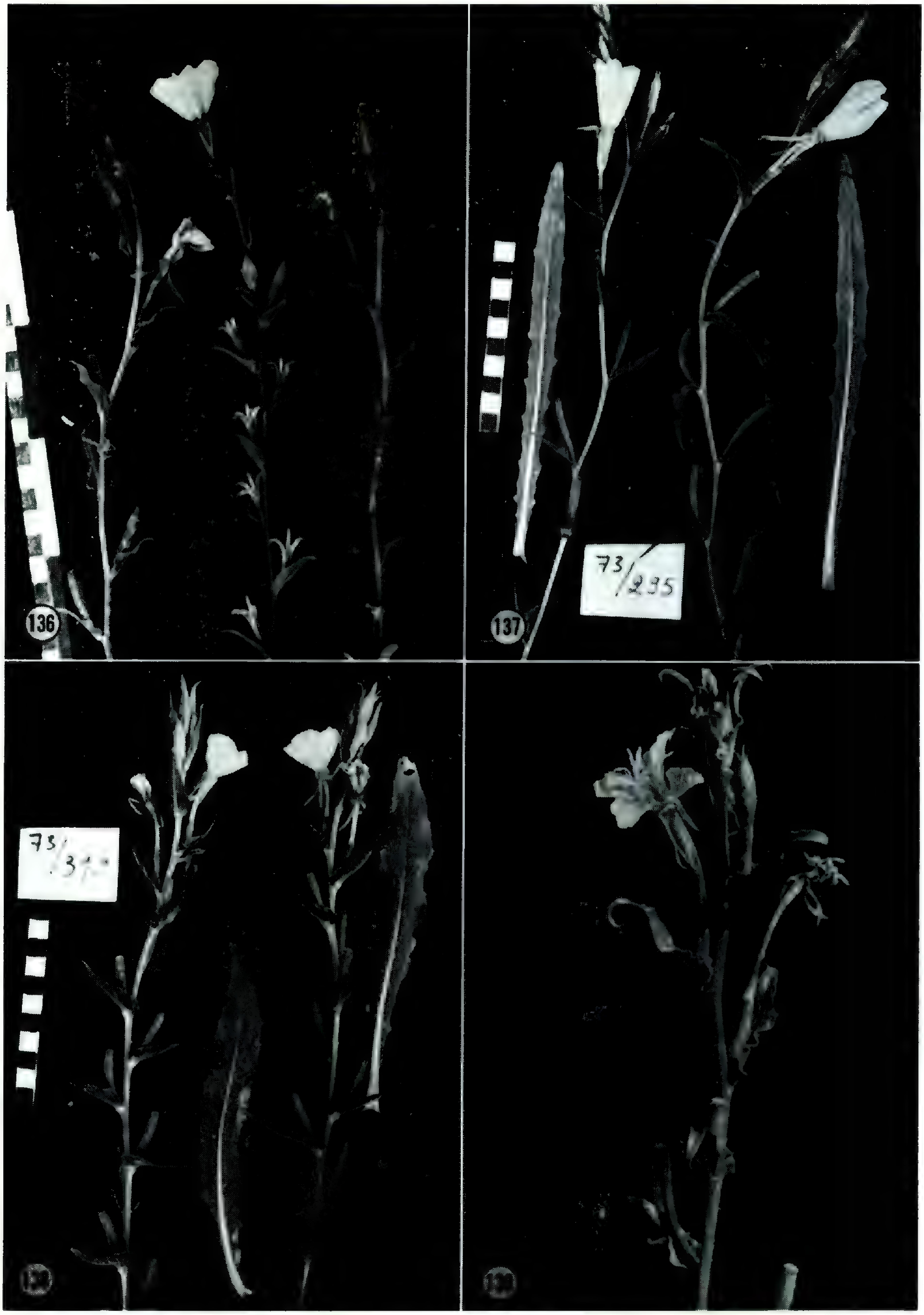
Oenothera mendocinensis is closely related to *O. odorata*, judged from their close similarity in habit, leaf form, and characteristics of the capsule and seeds. They have probably been derived from a common ancestor (Fig. 8), a suggestion which is consistent with their ranges.

It appears likely that the more generalized ancestral forms in series *Allochroa*—the closest living equivalents of which may be *O. mendocinensis* and *O. odorata*—were probably derived from generalized members of series *Renneria* in a center which on the basis of present-day distributions would appear to have been in and about the province of Mendoza. They then migrated to the south and southeast. The more advanced species (*O. indecora*, *O. ravenii*, *O. longiflora*, *O. affinis*), on the other hand, may have originated farther north, in the region of the provinces of Catamarca and Tucumán, and then spread predominantly toward the east and northeast and the region of the Chaco (Fig. 8).

15. **Oenothera odorata** Jacq., Icon. Pl. Rar. 3: *tab. 456.* 1795; Suppl. Coll. Bot. 5: 107. 1796.—FIGS. 37–40, 122–123, 175, 211.

Onagra undulata Moench, Suppl. Meth. Pl.: 287. 1802. TYPE: The herbarium of Moench apparently no longer exists.
Oenothera undulata W. T. Aiton, Hortus Kew. 2: 342. 1811. TYPE: Seeds from Port Desire, Argentina, 1790, cultivated at Kew (not seen).
O. odorata var. *virescens* Séringe in DC., Prodr. 3: 48. 1828. LECTOTYPE: Hort. parisiensis, 1816, *M. Brun in 1824* (G-DC). Grown from seed from the same source as the type of the species.
O. odorata var. *glaucescens* Séringe in DC., Prodr. 3: 48. 1828. LECTOTYPE: 28 August, *h.h.* (G-DC).
O. odoratissima Tausch, Flora 22: 557. 1839. LECTOTYPE: Cultivated in botanical garden, Herb. *V. Kosteletzky* (PRC, POM photograph); Munz, Amer. J. Bot. 22: 661. 1935.
O. mollissima sensu Hooker & Arnott, Bot. Beech. Voy. 23. 1841.
O. ibari Philippi, Anales Univ. Chile 84: 633. 1893. LECTOTYPE: Argentina, Prov. Santa Cruz, Lago Argentino (Lago Santa Cruz), 30 Jan. 1879, *E. Ibar* (SGO, GH photograph).
O. odorata f. *glabrescens*, *media* and *undulata* Spegazzini, Revista Fac. Agron. Univ. Nac. La Plata: 520. 1898. TYPES: not located.
O. mollissima sensu Macloskie, Rep. Princeton Univ. Exped. Patagonia 8(5, 3): 613. 1905.
Onothera polymorpha H. Lév. race *odorata* (Jacq.) H. Lév., Monogr. Onoth. 363. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.
O. polymorpha race *odorata* var. *undulata* (W. T. Aiton) H. Lév., Monogr. Onoth. 363. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.
O. polymorpha race *propinqua* (Spach) H. Lév. var. *ibari* (Philippi) H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909.
Oenothera mollissima subsp. *odorata* (Jacq.) Thell., Mitt. Bot. Mus. Univ. Zürich 58: 390. 1912.
Raimannia odorata (Jacq.) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.
Oenothera stricta sensu Munz, Physis 11: 285. 1933, pro parte; Amer. J. Bot. 22: 661. 1935, pro parte.

Erect annual herb, forming a rosette or the stem elongating after the formation of a few basal leaves, unbranched or with a branched main stem and prostrate or widely arcuate-spreading to obliquely ascending side branches arising from the rosette, 2.5–8 dm tall. Plants densely or sparsely strigillose and densely



FIGURES 136–139. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—136. *O. stricta* subsp. *stricta* (Chile, Cautín, *Stubbe in 1960*).—137. *O. stricta* subsp. *altissima* (Argentina, Río Negro, *Santarius 798*).—138. *O. stricta* subsp. *argentinae* (Argentina, Buenos Aires, *Santarius 346*).—139. *O. bahia-blancae* (Argent.na, Buenos Aires, *Santarius 457*).

or sparsely erect-villous or very densely to sparsely villous with erect long and short hairs, rarely sparsely glandular-pubescent. Rosette leaves linear to narrowly oblanceolate, acute, gradually narrowed to the petiole, 15–20 cm long, 0.5–1.5 cm wide; cauline leaves linear to very narrowly elliptic or narrowly lanceolate, acute, narrowly cuneate to acute at the base, short-petiolate or sessile, 5–18 cm long, 0.5–1.5 cm wide; bracts narrowly lanceolate to narrowly ovate, acute, truncate to subcordate at the base, 3–7 cm long, (0.3–)0.5–1.5 cm wide, shorter than, equal to, or longer than the capsule; leaves plane or the margins markedly to slightly undulate, irregularly serrulate. Inflorescence unbranched. Floral tube (1.5–)2–3 cm long. Buds lanceolate to narrowly ovate in outline, green or yellowish green, often flushed with red, 2–3 cm long, 0.5–1 cm thick; apices of the sepals erect, sharply divergent, or hornlike, 2–3 mm long. Petals very broadly obovate, retuse, 2–4.5 cm long. Anthers 9–14 mm long. Filaments 16–24 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, or long, the stigma held above the anthers at anthesis, 3.5–6.5 cm long. Stigma lobes 4–7 mm long. Ovary (1–)1.3–1.7 cm long. Capsule 3–5 cm long, 3–4 mm thick. Seeds elliptic in outline, light brown, 1.5–2 mm long, 0.5–0.8 mm thick. Self-compatible; autogamous in the complex heterozygotes, outcrossing in those chromosomal homozygotes in which the stigma is elevated above the anthers. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 14** or intermediate configurations at meiotic metaphase I). Flowering time: October–March.

Lectotype: Jacquin, Icon. Pl. Rar. 3: *tab. 456.* 1795. Cultivated in Vienna, seeds from Port Desire, ("Champion River"), Patagonia, Argentina, collected by Capt. Middleton and sent to Jacquin's son in 1793 by Sir Joseph Banks. Two specimens collected by Capt. Middleton are in the Forsyth Herbarium (NY), one from Port Desire, the other from Bay of San Dondo. Jacq., Coll. 107. 1796; Edwards, Bot. Reg. 2: *tab. 147.* 1816.

Distribution (Figs. 227, 242): Low elevations from sea level to 1,000 m altitude, in the provinces of Mendoza, Buenos Aires, Córdoba, La Pampa, Neuquén, Río Negro, Chubut, and Santa Cruz; ascending to 2,800 m elevation only in the cordilleras of Mendoza. In southern Chile it occurs only in the immediate vicinity of the border with Argentina.

Specimens examined from cultivated plants:

ARGENTINA. MENDOZA: Above El Peral, ca. 6 km NW of Tupungato, *Santarius 1574** (ring of 4, 5 bivalents) (DUSS, M, MO). Slopes of the Precordillera near Villavicencio, 2,500 m, *Santarius 1585, 1596*** (DUSS; *1585* also M, MO); 2,300 m, *Santarius 1614, 1624** (ring of 6, ring of 4, 2 bivalents), *1626, 1628, 1632, 1634* (ring of 10, 2 bivalents), *1637* (ring of 10, 2 bivalents) (DUSS; *1624* also CTES, M, MO); 1,750 m, *Santarius 1650* (ring of 6, 4 bivalents), *1651*** (DUSS; *1650* also MO). Dep. Las Heras, Caracoles de Villavicencio, *Hunziker 9073** (DUSS, M). BUENOS AIRES: Dunes near Mar del Plata, *Santarius 329** (ring of 4, 5 bivalents), *331, 333, 335, 336* (DUSS; *329* also CTES, M; *329, 331, 335* also MO). NEUQUÉN: Rocks ca. 500 m E of Piedra del Águila, 600 m, *Santarius 613* (ring of 8, 3 bivalents), *616* (ring of 8, 3 bivalents), *617*, 621*, 622, 624*, 625, 626, 627* (ring of 4, 5 bivalents), *629, 630*, 633*, 634, 635* (DUSS; *616, 617, 630* also CTES; *617, 621, 633* also M; *616, 617, 624, 626, 630* also MO). Río Limay at Ruta 237 ca. 75 km SSW of Piedra del Águila, *Santarius 644** (DUSS). Bank of Río Limay near Nahuel Huapí, 750 m, *Santarius 879**, 882***, *884* (DUSS). RÍO NEGRO: Bank of Río Limay at leaving of the Lago Nahuel Huapí, 750 m, *Santarius 887, 889, 892, 893***, 899, 902* (DUSS). Sandy and waste places along shore of

Lago Nahuel Huapí near the railroad station of San Carlos de Bariloche, 780 m, *Santarius 653* (ring of 12, 1 bivalent), *664* (ring of 4, 5 bivalents), *666, 668, 669* (ring of 10, 2 bivalents), *670** (ring of 10, 2 bivalents), *679* (ring of 6, 4 bivalents), *680** (ring of 6, 4 bivalents; ring of 8, 3 bivalents; ring of 10, 2 bivalents), *681, 682* (ring of 12, 1 bivalent), *686*, 688* (ring of 12, 1 bivalent), *689, 690, 693, 696*,*** (ring of 10, 2 bivalents), *697** (ring of 12, 1 bivalent), *701*, 702, 703*, 707*, 709, 713* (ring of 10, 2 bivalents), *714, 716*, 717*, 722* (ring of 4, 5 bivalents), *723* (ring of 8, 3 bivalents), *724*, 726*, 727, 732, 742, 746* (ring of 10, 2 bivalents), *749* (ring of 10, 2 bivalents), *751** (DUSS; *680, 716* also CTES; *653, 680, 689, 716* also M; *680, 686, 716, 746* also MO). E slope of Cerro Otto, 1 km W of Bariloche, 850 m, *Santarius 752*, 754, 755, 760* (ring of 10, 2 bivalents), *761* (ring of 6, ring of 4, 2 bivalents), *762, 765* (ring of 10, 2 bivalents), *766, 767** (ring of 10, 2 bivalents), *770, 771* (ring of 6, 4 bivalents), *777, 783*** (DUSS; *752* also CTES, M, MO); 950 m, *Santarius 788*, 790* (ring of 8, 3 bivalents) (DUSS). Slopes near Ruta 258, ca. 3 km N of Río Villegas, 67 km S of Bariloche, 700 m, *Santarius 800** (ring of 4, 5 bivalents), *801* (ring of 6, 4 bivalents), *802, 803, 806, 810**, 812, 814, 816, 819, 820* (ring of 8, 3 bivalents) (DUSS; *800* also M; *800, 801, 810* also CTES, MO). Estancia "San Ramón," W slopes at Río Limay, E of the bridge of Ruta 237 across the river, 750 m, *Santarius 854* (ring of 6, 4 bivalents; ring of 8, 3 bivalents; ring of 12, 1 bivalent), *866**, 868**, 872, 876, 878* (ring of 12, 1 bivalent) (DUSS; *878* also CTES, M, MO). CHUBUT: Sandy waste places in Villa Balneario Rada Tilly, ca. 14 km S of Comodoro Rivadavia, *Santarius 937* (ring of 12, 1 bivalent), *938* (ring of 12, 1 bivalent), *945* (ring of 12, 1 bivalent), *946, 947* (ring of 12, 1 bivalent), *948, 950* (ring of 12, 1 bivalent), *951, 953*, 954* (ring of 12, 1 bivalent), *957* (ring of 12, 1 bivalent), *958* (DUSS; *938, 950, 953, 957* also CTES, M, MO). SANTA CRUZ: Sandy places S of Puerto Deseado, at mouth of Río Deseado, *Santarius 959**, 961**, 963–967, 973**, 975, 979, 981**, 982**, 988* (ring of 8, 3 bivalents), *991, 994* (DUSS; *959* also CTES; *959, 982* also M; *959, 973, 981, 982* also MO). Sandy places in steppe with *Stipa*, 2 km NNE of Calafate at Lago Argentino, *Santarius 1162* (ring of 6, ring of 4, 2 bivalents; ring of 8, 3 bivalents), *1163, 1166, 1171* (ring of 4, 5 bivalents), *1175, 1179, 1182* (ring of 8, 3 bivalents), *1185* (ring of 6, 4 bivalents), *1190* (ring of 6, 4 bivalents), *1193* (ring of 6, ring of 4, 2 bivalents), *1194, 1196* (ring of 4, 5 bivalents) (DUSS; *1179* also M; *1175* also MO). Slope W of Arroyo Calafate, 350 m, *Santarius 1204** (ring of 8, 3 bivalents), *1206, 1208*, 1210, 1211* (DUSS; *1208* also M; *1208, 1210* also MO). Sandy places at E edge of Calafate, 200 m, *Santarius 1213*, 1216* (ring of 4, 5 bivalents), *1217, 1218* (ring of 8, 3 bivalents), *1220, 1228** (ring of 6, ring of 6, 1 bivalent), *1230** (ring of 4, 5 bivalents), *1233, 1239, 1241* (DUSS; *1213, 1230* also M; *1213, 1241* also MO). Near the airport of Calafate, 200 m, *Santarius 1245*, 1247, 1249, 1252* (DUSS; *1245* also CTES, M, MO). Stony and sandy places in the vicinity of Perito Moreno, 380 m, *Santarius 1257* (DUSS, MO). Lago Buenos Aires, at Río Los Antiguos W of Los Antiguos, 220 m, *Santarius 1322*, 1329* (ring of 12, 1 bivalent), *1331, 1332*, 1335* (ring of 10, 2 bivalents), *1336** (ring of 6, 4 bivalents; ring of 8, 3 bivalents; ring of 10, 2 bivalents) (DUSS; *1322, 1332, 1335*, also M; *1329, 1335, 1336* also CTES, MO).

CHILE. MAGELLANES: Ultima Esperanza near Salto de Paine, *Moore 990*** (DUSS, M, MO). 0–4 km E of Puente Lago Amarga, W of Lago Sarmiento, S of Lago Nordenskjold, *Santarius 1048**, 1049* (ring of 12, 1 bivalent), *1050* (ring of 12, 1 bivalent), *1052**, 1054, 1055, 1058*** (ring of 12, 1 bivalent), *1060, 1061* (ring of 12, 1 bivalent), *1064*** (DUSS; *1048, 1050* also CTES, M; *1048, 1050, 1058* also MO).

Representative specimens examined:

ARGENTINA. SAN JUAN: Calingasta, *Debenedetti* (SI-4859). MENDOZA: Villavicencio, 2,000 m, *Arque & Barkley in 1957* (LIL, NY); *Sleumer 469* (B, LIL), *Roig 5304* (CORD); *Ruiz Leal 1084* (Leal, LIL, POM); *Crovetto 9237* (BAB); *Wall in 1946* (S); *Mexia 04386* (GH, MO, UC); *Bartlett 19403* (GH, MICH, SI, US); *Senn 4443* (RSA). Los Hornillos, 2,600 m, *Barkley & Paci 240* (LIL, NY). Puente del Inca, 2,800 m, *Wall in 1946* (S). La Polvareda, 1850 m, *Palacios & Barkley 20 Mz331* (LIL, NY). Tunuyán, San Pablo, *Ruiz Leal 1812* (Leal, LIL, POM). Quebrada del Arroyo Manzano, 1,650 m, *Roig 4657* (CORD). Dep. Malalhue, Potimalal, 1,500 m, *Ruiz Leal 7492*, (Leal, LIL). Dep. Luján, El Carmelo, 2,000 m, *Cuezzo 2615* (LIL). Dep. San Rafael, Río Salado, Ciénaguita, *Rossi 294* (LIL). Dep. Tupungato, Canal Mártir near Toma, *Ruiz Leal 2794* (Leal, LIL, LP). Near San Pedro, *Gillies in 1824* (K). Paso Cruz, *Kuntze 59* (CORD, F). Dep. San Carlos, Quebrada Alvarado, *Covas 3492* (SI). Laguna Carrilauquen, *Kurtz 6109* (CORD, MO). Atuel Valley near El Sosneado, 1,600 m, *Böcher & Hjerting 881* (C). NEUQUÉN: Pulmaré, *Comber 388* (K). Between Catanlíl and Junín de los Andes at Río Aluminé, *Böcher et al. 1643* (C). Parque Nahuel Huapí, *De Barba 2106* (LIL, RSA); *Jacobsen 15* (POM). Manza near Zapala, *Ancibor 90245* (BAB).

Cohún-Có, *Comber 869* (K). Lago Huechulafquen, *O'Donell 2320* (LIL, NY, S, SI). Junction of Río Limay and Río Traful, *Cardini 46* (LIL). Cerro Lotena, 900 m, *Ammann 82* (F, M). Río Barrancas at Ruta 40 near Pehuenches, *Ancibor 90134* (BAB). San Martín de los Andes, *Dawson 1297* (BAA). Lago Lolog near San Martín de los Andes, *Scolnik 230* (RSA). RIO NEGRO: Parque Nahuel Huapí, *De Barba 750* (BM, LIL), *1462* (LIL, RSA); *Cardini 228* (US); *Giovanelli 13600* (BAB); *Bernicken in 1896* (LP), *Arnow 3761* (MO); *Fabris 1124* (BR); *Buchtien 1356* (AMD, BREM pro parte, GH pro parte, L, LE, LIL, LY, M, S, SI, US, W), *17* (POM). Banks of Río Negro near General Roca, *Krapovickas & Cristóbal 22414* (MO). Between Laguna de las Banduras and Fortín Fé, *N.N. in 1879* (CORD). El Condor near Viedma, *Cabrera et al. 19561* (LP, P). Carmen de Patagones, *Haumann in 1912* (BA). Dep. San Antonio, *Piccinini 1291, 1415, 1485, 1833* (BAB); *Hicken 37* (SI). Estuary of Río Negro, *N.N. 86* (LE). CHUBUT: Colonia Sarmiento, *O'Donell 3485* (LIL); *Cabrera 45* (LP). Puerto Madryn, *Dusén 5323* (SI); *O'Donell 3255* (LIL); *Soriano 2713* (BAB). Colonia San Martín, *Gerling 31* (POM). Gobernador Costa, *Birabén 580* (LP). Camarones, sea shore, *Aurelius 25* (S). Peninsula Valdez, *Rovereto 31-1537* (POM). Escalante, *O'Donell 3551* (LIL); *Kreibohm 110* (LP). Bahía Camarones (Port Sta. Elena), *Anderson 24 in 1826* (BM). Valley of Laguna Blanca, *Koslowsky 201* (BM, K, SI, Z). Esquel, *Castellanos in 1945* (F, LIL); *Eyerdam et al. 24575* (G, K, UC); *Kühnemann 647* (RSA). Corcovado, *Illin 6872, 6876* (BAB), *94* (BR, CORD, HBG, SI); *Soriano 3028* (CTES). Lago Futalaufquen, *Correa 4153* (BAB, UC); *Constance et al. in 1967* (BAA, MO); *Hicken 4, 14* (SI). El Maitén, *Meyer 9705* (LIL). SANTA CRUZ: Vicinity of Lago Argentino, *Dusén 5787* (S, SI); *Sleumer 1238* (LIL, US); *Boelcke 12509* (BAA, BAB); *Eyerdam et al. 24274* (G, GH, K, MO, SI, UC); *Scolnik 368* (RSA); *Furlong 99a* (GH, US), *5322* (NY); *Koslowsky 72* (CORD). Tehuelches, *Donat 54* (BM, G, GH, HBG, K, LIL, MO, NY, S, SI, UC, Z). Lago San Martín, *Rohmeder in 1945* (GH, LIL). San Julián, *Blake 56A* (LIL). Río Coyle, *Dauber 84* (POM). Río Gallegos, *Brown 62* (NY). Puerto Deseado, *Ancibor & Vizinis 4405* (BAA, MO); *Boelcke 12145* (BAA, BAB); *Eyerdam et al. 23869* (G, GH, K, MO, SI, UC), *O'Donell 3630* (LIL); *Anderson 49 in 1826* (POM). CÓRDOBA: Achiras, *Trelles* (SI-4853). LA PAMPA: Cerro Lihuel Calel, 400 m, *Burkart 20555* (P, SI); *Schwabe & Fabris 2028* (LP); *Krapovickas 3620* (BAB), *Krapovickas & Cristóbal 22384* (MO); *Troncoso in 1959* (SI); *Boelcke & Nicora 8120* (BAA, MO). General Acha, *Monticelli 10* (SI); *Troncoso in 1959* (SI). BUENOS AIRES: Balcarce, *Hunziker 3828* (POM). San Clemente near General Lavalle, *Cabrera 4921* (GH). Sierra La Tinta, *Spegazzini 40* (BAB). Quilmes, *Hicken in 1904* (SI). Mirimar, *Cabrera 5559* (LP). Mar del Sur, *Burkart 17876* (SI); *Nicora 17876* (SI, US). Pehuén-Có, *Correa 2299* (BAB); *Cabrera 14911* (LP, M); *Erettowi 2732* (MO); *Boelcke 11964* (SI). Bahía Blanca, *Ameghino 31-1628* (POM); *Job 1599* (NY). Bahía San Blas, *Fabris & Schwabe 5016* (CTES, M). Sierra Curamalal, *Spegazzini 18* (BAB); *Hohnberg in 1884* (CORD); *Burkart 4796* (BAA, CTES, MO); *Cabrera 5496* (LP); *Parodi 10355* (BAA, POM). Monte Hermoso, *Alboff in 1916* (LP); *Fabris & Schwabe 4817* (M); *Cabrera et al. 17055* (LP); *De Barba 633* (LIL); *Eskuche & Klein in 1968* (CTES). Quequén, *Castellanos 16092* (LIL); *Dawson 662* (LP, NY); *Rodríguez 828* (GH, LIL, NY). Necochea, *Nicora in 1961* (BAA), *7047* (MO); *Fabris & Schwabe 4759* (CTES, M, RSA); *Rodríguez 848* (GH, NY); *Eyerdam et al. 23709* (G, GH, K, UC). Sierra de la Ventana, *Alboff 124, 343* (CORD); *Cano & Cámara 227* (BAA, BAB); *Dawson 131* (LP), *Krapovickas 2958* (LIL, MO, RSA, SI); *Pastore 1205* (F, LIL, SI); *Abbiatti 4253* (NY). Olavarría, *Cabrera 20929* (P). Sierras del Azul, *Osten 152* (BREM).

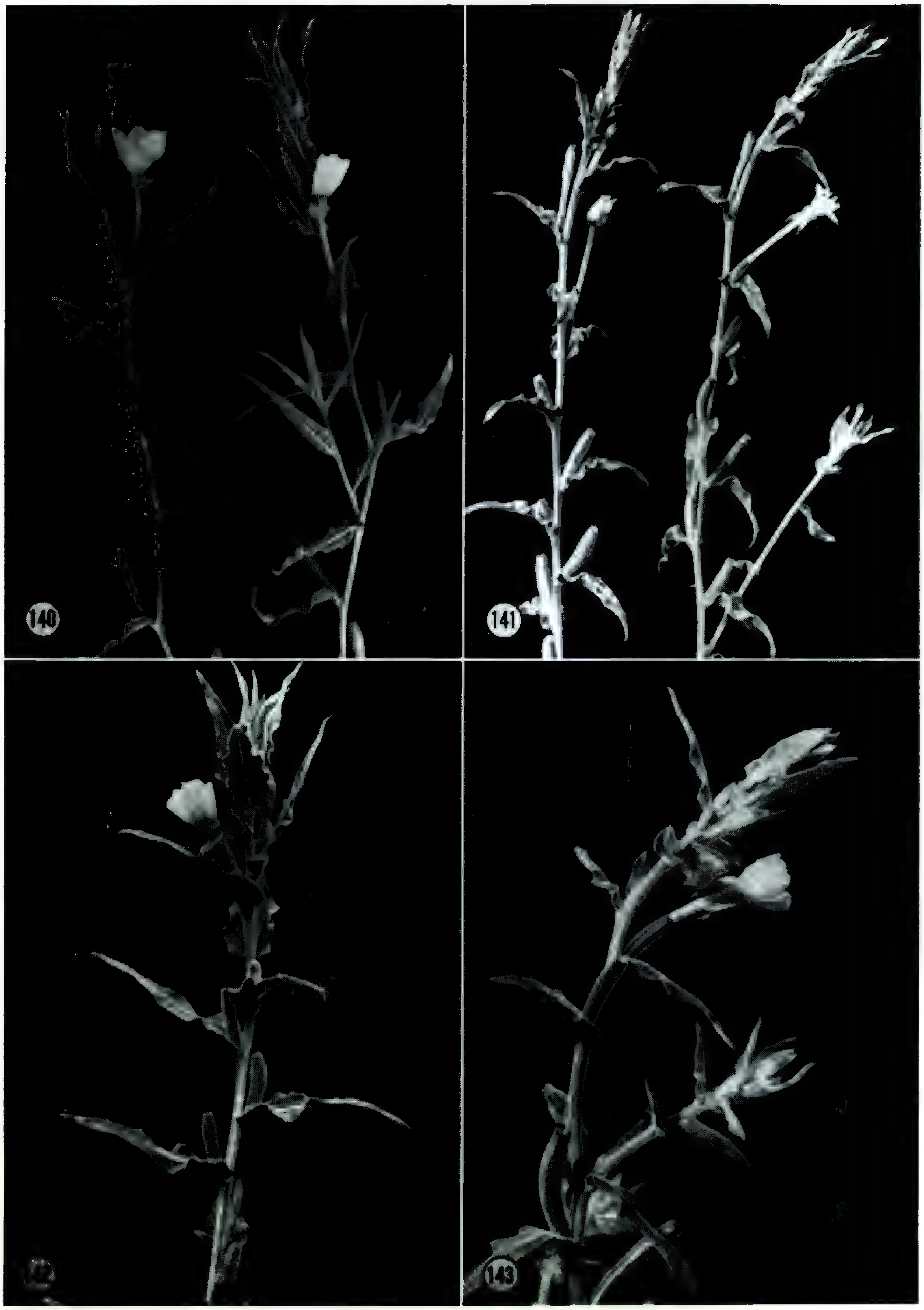
CHILE. AISÉN: Coihaique, *Rentzell 6129* pro parte (G, SI). Mina Silva near Lago Buenos Aires, *Heim in 1939* (Z). MAGELLANES: Puerto Prat, *Hicken 106* (SI).

Specimens from plants cultivated in gardens:

Hort. Kew, seeds from Port Desire, Argentina, *in 1791* (BM). Botanical Garden Paris, *in 1814*, Herb. *Cambessedes* (MPU). Botanical Garden Munich, Germany, *in 1814*, Herb. *Martius* (BR). Botanical Garden Arlary, *in 1827* (GH). Botanical Garden Munich, *in 1832* (M; as *O. undulata* Horti). Munich, *in 1833*, (BR; as *O. undulata*). Warsaw, Poland, *in 1834* (LE; as *O. undulata*). Botanical Garden Paris, *in 1842* (BR). Leningrad, USSR, *in 1847* (LE; as *O. dubia* F.M.). Leningrad, *in 1848* (LE; as *O. cognata*). Botanical Garden of Vienna, seeds from Berlin, *in 1856* (W; as *O. villosa*). Cultivated at Nymans, Sussex, England, 1929, *Comber 388* (K). Cultivated in Botanical Garden, Leningrad, seeds from *D. Nolte*, 1847 (LE; as *O. dubia* F.M.). Cultivated in Botanical Garden, Leningrad, 1847 (LE; as *O. cognata*).

Oenothera odorata reported in the literature from outside of South America:

GERMANY: Hegi (1925; pt. 2: 864).



FIGURES 140–143. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—140. *O. picensis* subsp. *picensis* (Argentina, Mendoza, *Santarius 1554*).—141. *O. picensis* subsp. *cordobensis* (Argentina, Jujuy, *Santarius 1845*).—142. *O. picensis* subsp. *bonariensis* (Argentina, Buenos Aires, *Santarius 370*).—143. *O. montevidensis* (Uruguay, Montevideo, *Santarius 1*).

Oenothera odorata is characterized by its large flowers with a relatively short floral tube; long, narrow fruits; and bracts broadly rounded at the base. Aside from *O. magellanica*, it is the only frequent member of the subsection in southernmost South America. This species is extraordinarily variable, but it is impossible to arrange its variability into an inclusive and useful taxonomic system; consequently, no infraspecific taxa are recognized. Especially pronounced is the variability in habit, hue of the stems and leaves, leaf shape, and pubescence.

Plants with plane leaves grow intermixed with others with somewhat undulate leaves in the same populations, in which intermediates also occur. Reddish or greenish coloration of the above-ground parts segregates in a Mendelian fashion, as it does in other species of the genus.

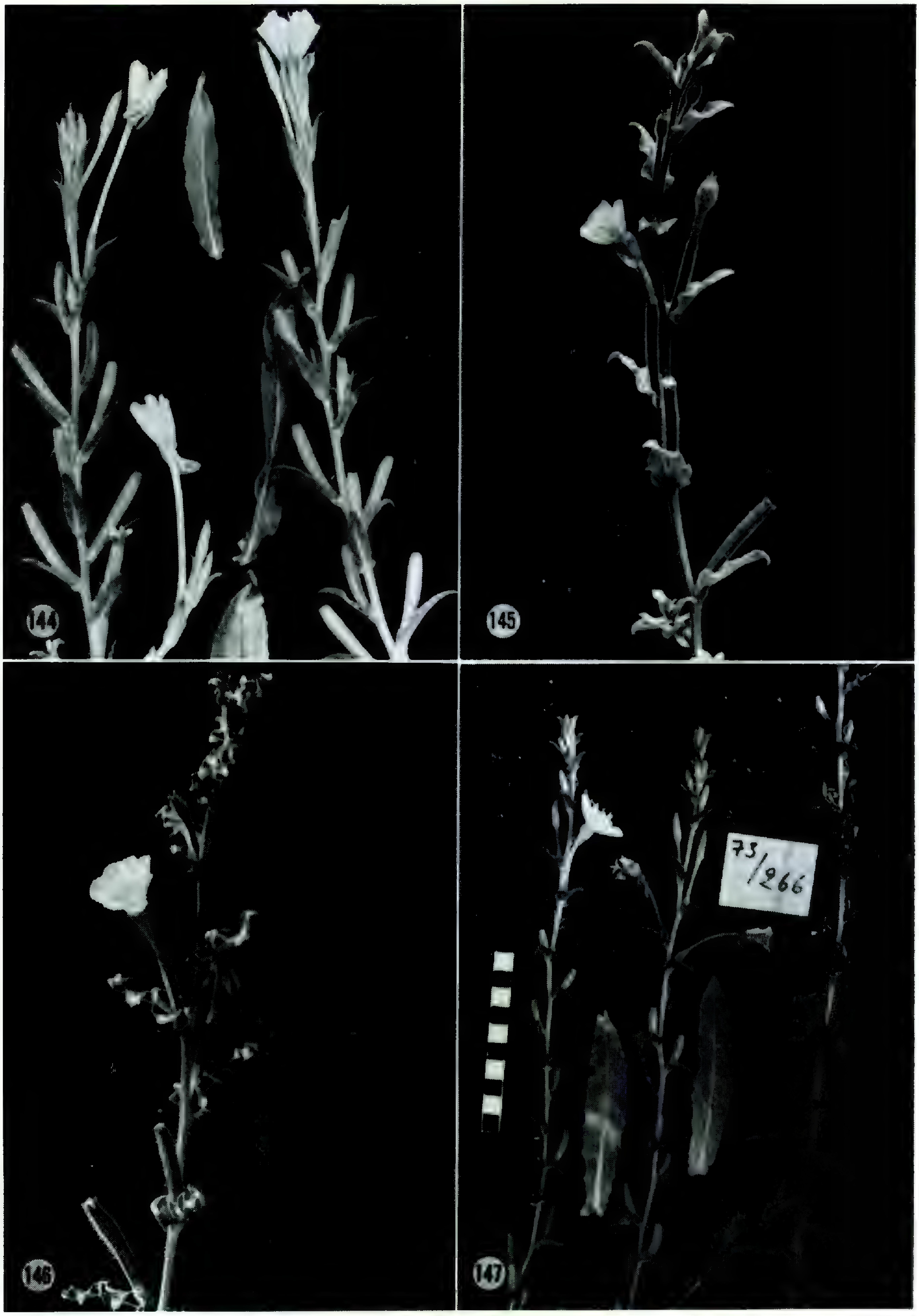
Plants with strigillose pubescence are completely absent in the northeast part of the range, in the province of Buenos Aires, but are widespread elsewhere. They predominate in the south, whereas populations consisting exclusively of plants with villous pubescence are more frequent in the north. Populations of this species in the province of Buenos Aires consist mainly of plants with an almost woolly pubescence, and are distinctive in this respect. Such populations have not been accorded taxonomic recognition, however, because they include, in addition to those with woolly pubescence, others which are identical to the less densely pubescent forms that are frequent in the provinces of La Pampa, Neuquén, and Río Negro.

The hairs that make up the so-called strigillose pubescence of *O. odorata* are not typical of those normally included in this category of pubescence in the species of series *Renneria*. In this series strigillose hairs are ca. 0.2 mm long and appressed closely to the stem, whereas in *O. odorata* they are about twice as long and generally erect, with only the tip curved toward the stem. The pubescence in *O. odorata* could therefore with justification be regarded as intermediate between strigillose and villous in character.

Oenothera odorata is extremely variable in its chromosomal configurations. Plants with 7 bivalents and all configurations up to and including complex heterozygotes with a ring of 14 occur. In the vicinity of Comodoro Rivadavia, Chubut Prov., the essentially stable configuration ring of 12 + 1 bivalent seems to have become predominant. This situation has been discussed further on p. 437.

16. **Oenothera ravenii** Dietrich, sp. nov.—FIGS. 6, 41–43, 47–49, 124–127, 176, 212.

Herba annua vel biennis, erecta, rosulata, simplex vel caulis principalis ramosus et ramis plerumque late arcuate vel rariore oblique e rosula ascendentibus, 5–10 dm alta. Plantae dense villosae, praecipue inferiore, sparseque glanduloso-pubescentes vel parce ad sparse strigulosi praecipue inferiore. Folia rosulae cultrata vel anguste oblanceolata, plerumque breviter acuta, basi acuta vel truncata, sessilia, 8–20 cm longa, 1.5–3 cm lata; folia caulina cultrata ad anguste oblonga vel lanceolata, acuta, basi truncata vel subcordata, sessilia, 3–15 cm longa, 0.8–1.5(–2) cm lata; bractea anguste ovata vel ovata, acuta, basi truncata vel subcordata, sessilia, plerumque quam capsulam subtena multo breviora, raro ad eam subaequalia, 1.5–3 cm longa, 0.5–1.5 cm lata; folia subintegria vel irregulariter obtuseque serrata, saepe marginibus praecipue in bracteis rubrescentibus. Inflorescentia simplex vel ramosa. Tubus floralis (2–) 3–5.5(–6.5) cm longus. Gemmae ambito oblongae vel lanceolatae, 1–3.5 cm longae, 5–11 mm



FIGURES 144–147. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—144. *O. pseudolongiflora* (Argentina, Buenos Aires, *Santarius 271*).—145. *O. parodiana* subsp. *parodiana* (Uruguay, Florida, *Santarius 211*).—146. *O. parodiana* subsp. *parodiana* (Argentina, Buenos Aires, *Santarius 468*).—147. *O. parodiana* subsp. *brasiliensis* (Argentina, Entre Ríos, *Burkart 23423*).

crassae, plerumque junctura sepalorum tubo florali rubro-fasciatae, flavae vel flavido-virescentae, saepe rubrae. Sepala saepe dense vel sparse rubro-maculata; apices sepalorum erecti vel divergentes, 1–3 mm longi. Petala latissime obovata, lutea, saepe basi rubro-maculata, 1.2–5 (–5.5) cm longa. Stylus longus, stigmate sub anthesi supra antheras elevato, vel brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.5–2.5 cm longum. Capsula 2.5–3.5 cm longa, 3–4 mm crassa, plerumque ab caulo directo subperpendicularo curvatum. Semina ambito elliptica vel rotundata, fusca, 1–1.5 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica, heterozygotica complexa, vel intermedia.

Erect annual or biennial herb, forming a rosette, unbranched or with a branched main stem and side branches which are usually widely arcuate but sometimes obliquely ascending from the rosette, 5–10 dm tall. Plants ± densely villous, especially below, and sparsely glandular-pubescent or moderately to sparsely strigillose, especially below. Rosette leaves cultrate to narrowly oblanceolate, mostly short acute, acute to truncate at the base, sessile, 8–20 cm long, 1.5–3 cm wide; cauline leaves cultrate to narrowly oblong or lanceolate, acute, truncate to subcordate at the base, sessile, 3–15 cm long, 0.8–1.5(–2) cm wide; bracts narrowly ovate to ovate, acute, truncate to subcordate at the base, sessile, mostly much shorter than the capsule they subtend, rarely ± the same length, 1.5–3 cm long, 0.5–1.5 cm wide; leaves plane or undulate at the margins, subentire or irregularly serrate with blunt teeth, often reddish along the margins, especially the bracts. Inflorescence branched or unbranched. Floral tube (2–)3–5.5(–6.5) cm long. Buds oblong to lanceolate in outline, 1–3.5 cm long, 5–11 mm thick, usually reddish at the junction of the sepals with the floral tube, yellow or yellowish green, often flushed with red. Sepals often densely or sparsely flecked with red; apices of the sepals erect or divergent, 1–3 mm long. Petals very broadly obovate, yellow, often with a red spot at the base, 1.2–5 (–5.5) cm long. Anthers 6–13 mm long. Filaments 8–27 mm long. Style long, the stigma held above the anthers at anthesis, or short, the anthers shedding pollen directly on the stigma at anthesis, 3–9 cm long. Stigma lobes 4–9 mm long. Ovary 1.5–2.5 cm long. Capsule 2.5–3.5 cm long, 3–4 mm thick, mostly curved directly outward from the stem. Seeds elliptic to rotund in outline, brown, 1–1.5 mm long, 0.5–0.7 mm thick. Self-compatible; outcrossing in those plants, all chromosomal homozygotes, in which the stigma is held above the anthers at anthesis, and self-pollinating in the rest. Gametic chromosome number, $n = 7$ (7 bivalents, ring of 14 or intermediate configurations at meiotic metaphase I).

Type: Grown from seed and cultivated in the Botanical Garden of Düsseldorf, Germany, 15 Aug. 1972. Source: Brazil, State of Rio Grande do Sul, Pelotas, 1966, *E. J. Hackbart* (MO-2155712, holotype; CTES, DUSS, M, isotypes).

Distribution (Figs. 225–226, 228, 243): In Brazil from Rio Grande do Sul north to the state of São Paulo; in Uruguay in the provinces of Salto, Cerro Largo, Rocha, Lavalleja, and Montevideo; in Argentina in the provinces of Misiones, Corrientes, Entre Ríos, Santa Fé, Buenos Aires, and Córdoba; in central Paraguay; and in Chile from Valdívia to Valparaíso.

This new species is dedicated to Peter H. Raven (1936–). Among its characteristics are the short, red-margined bracts and the sessile, usually oblong

rosette and cauline leaves. Within this species subsp. *ravenii* is chromosomally homozygous, whereas subsp. *argentinae* and subsp. *chilensis* are entirely chromosomally heterozygous, but deriving both of their complexes from *O. ravenii*. Hybrids of chromosomal heterozygotes with homozygotes within this species yield only two closely similar phenotypes, both easily assignable to *O. ravenii*, in the F_1 generation. Similarly, hybrids with other homozygous species show that all elements included here within *O. ravenii* agree closely genetically despite their chromosomal differences.

Key to the Subspecies

1\. Petals 2.5–5 cm long; stigma usually elevated above the anthers at anthesis; buds 2–3.5 cm long .... 16a. subsp. *ravenii*

1′. Petals 1.2–3 cm long; stigma surrounded by the anthers at anthesis; buds 1–2 cm long.

2\. Buds lanceolate in outline, 1–1.7 cm long; petals 1.2–2 cm long; seeds 1–1.3 mm long .... 16b. subsp. *argentinae*

2′. Buds oblong in outline, 1.5–2 cm long; petals 2–2.5 cm long; seeds 1.3–1.5 mm long .... 16c. subsp. *chilensis*

16a. **Oenothera ravenii** subsp. **ravenii**.—Figs. 6, 41–43, 124–125, 176, 212.

O. mollissima L. var. *paraguayensis* Chod., Bull. Herb. Boissier 7(9, app. 1): 71. 1899. LECTOTYPE: Paraguay, margins of forests near Cordillera de Altos, July (1885–1895), *E. Hassler 338* (G, holotype; G, P, isotypes); Hassler, Bull. Soc. Bot. Genève, sér. 2, 5: 274. 1913.

O. mollissima sensu Chodat, Bull. Herb. Boissier 7(9, app. 1): 71. 1899.

O. longiflora sensu Munz, Physis 11: 285. 1933, pro parte; Amer. J. Bot. 22: 663. 1935, pro parte; Comun. Bot. Mus. Hist. Nat. Montevideo 1(10): 35. 1943, pro parte; Fl. Brasílica 9(41): 55. 1947.

O. parodiana sensu Munz, Amer. J. Bot. 22: 662. 1935, pro parte.

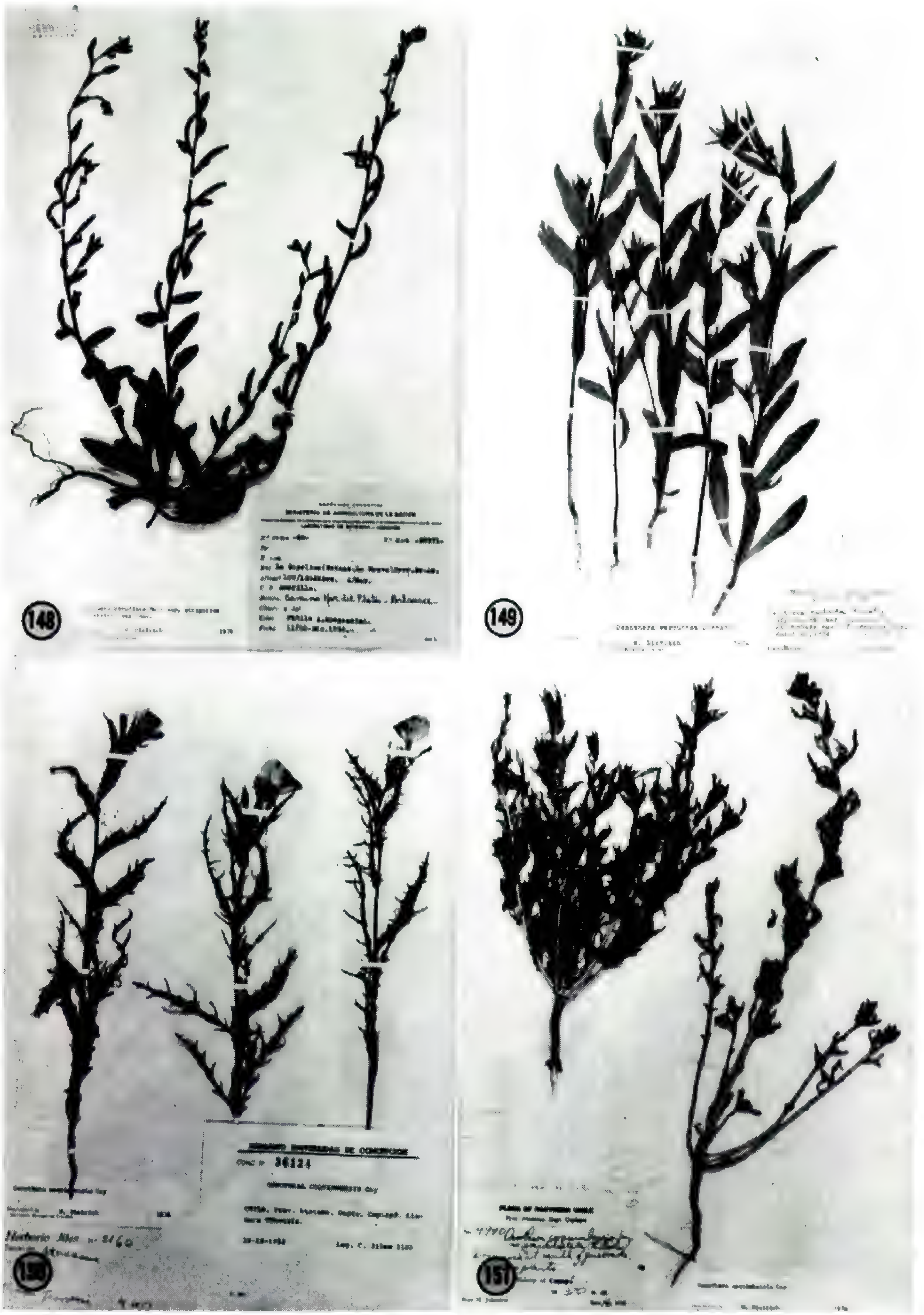
Rosette leaves cultrate to narrowly oblong or oblanceolate. Floral tube 3–5.5(–6.5) cm long. Buds lanceolate in outline, 2–3.5 cm long, 7–11 mm thick. Sepals reddish around the edges and often flecked with red on the surface; apices of the sepals 2–3 mm long. Petals 2.5–5 cm long. Anthers 8–13 mm long. Filaments 18–27 mm long. Style long, rarely short, the stigma usually elevated above the anthers at anthesis, 5.5–9 cm long. Stigma lobes 5–9 mm long. Ovary 1.5–2.5 cm long. Seeds 1.3–1.5 mm long, broadly elliptic in outline. Self-compatible but mostly outcrossing or self-pollinating and complex heterozygote. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 14** or small rings at meiotic metaphase I). Flowering time: October–June.

Distribution (Figs. 225, 243): Occurs in Brazil from Rio Grande do Sul north to Minas Gerais; in Uruguay in the provinces of Salto, Cerro Largo, Rocha, Lavalleja, and Montevideo; in central Paraguay; and in Argentina in the provinces of Misiones, Corrientes, Entre Ríos, and Santa Fé.

Specimens examined from cultivated plants:

BRAZIL. RIO GRANDE DO SUL: Pelotas, *Hackbart 1966** (ring of 6, 4 bivalents; ring of 8, ring of 4, 1 bivalent) (CTES, DUSS, M, MO). SANTA CATARINA: Coast near Ararangua, *Schultz in 1970* (ring of 4, 5 bivalents) (DUSS).

ARGENTINA. MISONES: At Ruta 12 near San Ignacio, *Conrad & Dietrich 26, 27* (ring of 6, 4 bivalents), *24* (2 rings of 6, 1 bivalent) (DUSS). CORRIENTES: Est. Garruchos near Santao Tomé, *Krapovickas 21464*** (DUSS).



Figures 148–151. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—148. *O. parodiana* subsp. *strigulosa* (Argentina, Buenos Aires, *Spegazzini in 1938*).—149. *O. verrucosa* (Peru, Arequipa, *Munz 15540*).—150. *O. coquimbensis* (Chile, Atacama, *Jiles 2160*).—151. *O. coquimbensis* (Chile, Atacama, *Johnston 4990*).

PARAGUAY. CORDILLERA: Roadside near Altos, ca. 10 km NE of San Bernardino, *Conrad & Dietrich 30***, *36*** (DUSS). Ca. 4 km SSE of San Bernardino, *Conrad & Dietrich 39*** (DUSS). CENTRAL: 3 km S of Aregua, *Conrad & Dietrich 50***, *53*** (DUSS).

Additional specimens examined:

BRAZIL. MINAS GERAIS: High fields in the Serra do Pieú, 1,800 m, *Schwacke 5248* (BR). SÃO PAULO: *St.-Hilaire 1498* (P). PARANÁ: Eng. Bley near Lapa, *Hatschbach 1067* (S, US). Between Jaguariaiva and Senges, *Hatschbach 9064* (HB, L). Roca Nova near Piraquara, *Hatschbach 1898* (RSA). Ponta Grossa, *Schwacke in 1874* (R); *Hoehne 23248* (SP). Curitiba, *Galvão in 1884* (R); *Stellfeld 1112* (SP). 50 km W of Guarapuava, 1,000 m, *Reitz & Klein 17713* (US). Agua Sta. Clara near Guarapuava, *Pereira 7967* (HB). Porto Amazonas, *Gurgel in 1929* (BR); *Gimpel 16163* (BR). Vila Velha, *Pereira & Pabst 7547* (M); *Dusén in 1904* (S); *N.N. in 1904* (R); *Hertel 52325* (SP); *Pereira 8272* (BR, HB). *Santa Catarina*: Bom Retiro, 1,650 m, *Smith & Klein 10435* (HBR, RSA, US). Ponte Alta near Curitibanos, 800–900 m, *Smith & Klein 8246* (HBR, NY, R, RSA, US). Agua Doce near Rio Chapeco, 12 km S of Horizonte, *Smith & Klein 13550* (HBR, RSA). Fazenda de Laranja, S. Joaquim near Bom Jardim, 1,400 m, *Reitz & Klein 7735, 7977* (HBR). Palhoca near Maciambu, *Reitz & Klein 980* (HBR). Garopaba, *Klein & Bresolin 8855* (HBR). Palmas near Joaçaba, 52 km W of Caçador, 1,000–1,300 m, *Smith & Reitz 9153* (US). Cangicas near Araranguá, 50 m, *Reitz C254* (BR, HBR). Sombrio near Araranguá, 10 m, *Reitz C1308* (GH, HBR). Campos Novos, 1,000 m, *Klein 4187* (HBR, RSA). RIO GRANDE DO SUL: Montenegro, *Henz 32563* (LIL). Uruguaiana, *Palacios & Cuezzo 210* (LIL). Between Cacapava do Sul and Morro Perao, *Palacios & Cuezzo 1449* (LIL). Between Alegrete and Capivari, *Palacios & Cuezzo 1919* (LIL). Itapoan, *Rambo 44448* (LIL). Near Farroupilha, *Rambo 42543* (LIL). Cerro de San Martinho near Sta. Maria, *Vidal 1508* (R). Rio Pardo, *Vidal 01570* (R). Between Capão de Canôa and Osório, *Nelson in 1970* (BR). Caaró near São Luiz, *Rambo 53349* (B). Lagoa Vermelha, *Rosengurtt 9078* (MVFA). Est. do Jaran near Quarai, *Rambo 26320* (LIL). Passo do Socorro near Vacaria, *Rambo 51383* (HBR). Pelotas, *Beetle 2236* (US); *Costa Sacco 690* (F, HB, R). Piratiny near Pelotas, *Malme 159* (S). S. Leopoldo, *Rambo 293* (LIL). Porto Alegre, *Molfino in 1898* (POM); *S. Barbara in 1835* (BR); *Rambo 27040* (LIL). Gloria near Porto Alegre, *Bornmüller 47* (GH); *Rambo 6461* (SP).

URUGUAY. CERRO LARGO: Río Branco, *Herter 2104* (F, MO, NY, US, Z). Bañado de los Burros, *Flossdorf 1* (POM, SI). Arroyo Zapallar, *Praderi 742* (LIL). SALTO: Thermal Springs of Arapey, *Rosengurtt 10569* (MVFA). Paso del Arroyo Las Cañas, *Rosengurtt B1058* (POM). ROCHA: Castillos, *Herter 987938* (POM). E coast of Uruguay, *St.-Hilaire 2213* (P). LAVALLEJA: Road to Puma near Minas, *Osten 4490* (G). C. Verdún near Minas, *Berro 6246* (MVFA). MONTEVIDEO: Punta Gorda, *Osten 22088* (GH).

ARGENTINA. MISIONES: Candelaria, *Bertoni 2463* (LIL); *Descole 3270* (LIL); *Sesmero 83* (LIL). Loreto near Candelaria, 290 m, *Montes 58B* (US). At Ruta 14 near Arroyo Garupá Norte, *Krapovickas et al.* (CTES). Garupá near Candelaria, *Bertoni 4734* (LIL). Pindapoy near Candelaria, *Bertoni 3862* (LIL). Santa Ana, *Bertoni in 1944* (LIL); *Sesmero 168* (LIL, NY); *Rodríguez 671* (BA, LIL, POM, SI, UC); *Schwarz 632* (LIL, NY, UC); *Montes 1516* (RSA); *Rodríguez 158* (LIL). San José, *Sesmero 241* (LIL). Posadas, *Gallando 3739* (SI); *Bertoni 1514* (LIL). Mártires near Posadas, 130 m, *Bertoni 5724* (LIL). Posadas, *Ekman 2029* (G, LD, S, US). Cerro Corá, *Crovetto 9492* (BAB). Puerto Leoni near Cainguas, *Schwarz 1575* (LIL). Apostoles, *Ibarrola 1051* (BR, LIL, NY). Santa Irene near San Javier, *Bertoni 526* (LIL). Corpus near Santa Ana, *Bertoni 1866* (LIL). Sto. Tomás, 160 m, *Bertoni 4696* (LIL). Santa Inés, *Meyer 11439* (LIL). Concepción, *Schwarz 3566* (LIL, RSA). Arroyo Jabebiri, *Meyer 11512* (LIL). Villa Samis, *N.N. in 1944* (LIL). El Dorado near Iguazú, *Schwartz 2042* (LIL). Puerto Wanda near Iguazú, *Montes 9591* (LIL). Puerto Istuela, *Montes 10117* (LP). Arroyo Apepú near San Ignacio, *Schwarz 2882* (LIL). Menóchio near San Ignacio, *Schwarz 1255* (LIL). San Ignacio, *Medina 212* (LIL, RSA). CORRIENTES: Estancia "Santa Teresa," *Pedersen 93* pro parte (S, US). Est. "Garruchos" near Santo Tomé, *Pedersen 9229* (C); *Krapovickas et al. 21464* (MO). At Ruta 14 near Gob. Virasoro, *Krapovickas et al. 16692, 16753* (CTES). Est. San Francisco, 23 km NW of Gob. Virasoro, *Krapovickas et al. 17217* (CTES). Paso Pucú near Concepción *Pedersen 7482* (C). Baibiene, *Castellanos 34445* (RSA). S. Roqueito near Mercedes, *Irigoyen 71* (CTES). San Carlos near Ituzaingó, *Krapovickas et al. 17995* (CTES). Yahápe at Ruta 12 near Berón de Astrada, *Krapovickas et al. 16537* (CTES). ENTRE RÍOS: Concepción del Uruguay, *Lorentz in 1876* (BM). SANTA FÉ: Road to Requoncista, *Job 974* (NY).

PARAGUAY. Cordillera de Altos, *Fiebrig 434* (F, G, GH, HBG, K, L, LY, M); *Hassler 338* (G, P), *744* (G, K, P). San Bernardino, *Hassler 3343* (BM, G, GH, K, LY, NY, P, W). Near

Igatimi, *Hassler 5567* (BM, G, GH, K, LIL, LY, MO, MPU, P, S, UC, W); *Töppen in 1883* (HBG). Vicinity of the river Y-aca, *Hassler 6879* (BM, G, GH, K, LIL, LY, MICH, MO, MPU, NY, P, S, UC, W). Vicinity of the lake Ypacaray, *Hassler 12486* (BM, C, F, G, GH, K, L, LIL, LY, MICH, MO, NY, S, UC, US, Z). Villa Elisa, *Pedersen 5125* (C). Caáguazú, *Balansa 2220* (G, P, RSA); *Hassler 8996* (BM, G, K, NY, W); *Töppen in 1883* (HBG). Tapytá, *Jörgensen 4754* (F, MO, NY, POM, S, SI, US). Sapucaí, *Götzsche in 1891* (CORD). Pirareta near Paraguarí, *Sparre & Vervoorst 173* (LIL). Chololo near Paraguarí, *Sparre & Vervoorst 613* (LIL). Encarnación, 110 m, *Bertoni 4524* (LIL); *Schrottky 116* (LIL).

Early specimens from plants cultivated in Botanical Gardens:

Rovig in 1818 (CORD; as *O. longiflora*). From the Garden of Mr. Ohm at Berlin, *Bauer in 1838* (CORD; as *O. sellowiana*). From Botanical Garden at Berlin, *Bauer in 1842* (CORD; as *O. sellowiana*).

Oenothera odorata and *O. featherstonei* are the only entities that regularly exceed *O. ravenii* subsp. *ravenii* in flower size. In this subspecies, plants with red-flecked and entirely green sepals grow intermixed in the same populations, and the characteristic seems to segregate in a Mendelian fashion. Plants from Brazil, Uruguay, and the provinces of Corrientes and Entre Ríos in Argentina are moderately pubescent, whereas those from the Province of Misiones in Argentina are very densely pubescent, especially in their lower portions.

On the map of distribution of the *ravenii*-complex (Fig. 243), it can be seen that this chromosomal complex exists in homozygous form only in the northeastern portion of the range. Evidently, this complex combines readily with others as discussed under species no. 23, 27, 28, 36, 37 and 41. As the ancestors of *O. ravenii* migrated east from a probable area of origin in the vicinity of Tucumán, they seem to have hybridized readily with others, and the homozygotes persist today only at the very margins of the range.

Just as in *O. odorata*, the existence of an array of chromosomally differentiated homozygotes may be inferred within this entity, the hybridization of which has given rise to the complex heterozygotes. In Düsseldorf two chromosomally homozygous plants (*72-1227a* and *72-1228*) from the same locality near Pelotas were crossed and gave rise in the F_1 generation to a plant (*73-576*) with a ring of 14 chromosomes, showing that such potentiality existed also within the original population.

16b. **Oenothera ravenii** subsp. **argentinae** Dietrich, subsp. nov.—FIG. 126.

O. parodiana sensu Munz, Physis 11: 283. 1933, pro parte; Amer. J. Bot. 22: 662. 1935, pro parte.

O. stricta sensu Munz, Physis 11: 285. 1933, pro parte.

Folia ut in subsp. *ravenii*. Tubus floralis 1.8–3.5 cm longus. Gemmae ambito lanceolatae, 1–1.7 cm longae, 5–7 mm crassae. Sepala rubro-marginata, saepe etiam rubro-maculata; apices sepalorum 1–2 mm longi. Petala 1.2–2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.3–1.5 cm longum. Semina 1–1.3 mm longa, 0.5–0.7 mm crassa, ambito rotundata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Leaves as in subsp. *ravenii*. Floral tube 1.8–3.5 cm long. Buds lanceolate in outline, 1–1.7 cm long, 5–7 mm thick. Sepals with red margins, often also flecked with red; apices of the sepals 1–2 mm long. Petals 1.2–2 cm long. Anthers 6–8 mm long. Filaments 12–15 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 3–4.5 cm long. Stigma lobes 4–5 mm

FIGURES 152–153. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—152. *O. arequipensis* (Peru, Arequipa, *Mexia 04167*).—153. *O. featherstonei* (Peru, Lima, *Weberbauer 5217*).

long. Ovary 1.3–1.5 cm long. Seeds 1–1.3 mm long, 0.5–0.7 mm thick, rotund in outline. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 12 and 1 bivalent** at meiotic metaphase I). Flowering time: October–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Córdoba, Copina near Córdoba, Dec. 1961, *G. Göpel* (MO-2155709, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 228): In Brazil, so far known only from the state of Rio Grande; the southern departments of Canelones, Maldonado, and Florida in Uruguay; and the provinces of Entre Ríos, Buenos Aires, and Córdoba in Argentina.

Specimens examined from cultivated plants:

BRAZIL. RIO GRANDE DO SUL: Pelotas, *Hackbart in 1966** (DUSS, M); *Hackbart in 1967**,** (DUSS).

ARGENTINA. ENTRE RÍOS: Concepción del Uruguay, *Burkart in 1961** (DUSS). CÓRDOBA: Copina near Córdoba, *Göpel in 1961** (DUSS, M, MO). BUENOS AIRES: Mar de la Plata, *Santarius 342** (CTES, DUSS, MO).

URUGUAY. FLORIDA: Florida, *Hecht 1964-31** (DUSS). Mansavillagra, *Santarius 231** (CTES, DUSS, MO).

Additional specimens examined:

BRAZIL. RIO GRANDE DO SUL: Near Caçapava, road to São Sepé, *Rosengurtt 8736* (MVFA).
URUGUAY. MONTEVIDEO: Montevideo, *Arillaga 721* (MVFA). FLORIDA: Casuja, *Borsani 5564* (MVFA). CANELONES: Arroyo Sarandi, *Izaguirre 154* (MVFA).

ARGENTINA. ENTRE RÍOS: Concepción del Uruguay, *Lorentz in 1876* (GH). BUENOS AIRES: Vicinity of Junín, *Saint-Ives 173* (G). Sierra de la Ventana, *N.N. 12789* (LP). Est. San Juan, 30 km S of Buenos Aires, *Eyerdam 23037a* (G, GH, K, MO, UC). 20 km N of Mar del Plata, road to Balcarce, *Eyerdam et al. 23644, 23669* (GH, K, UC). "La Brava" near Balcarce, *Lourteig 162* (LIL); *Capurro in 1941* (LIL). Cerro El Sombrerito near Tandil, 550 m, *Huidrobo 1770* (LIL, NY). El Dia, *King 263* (BM). Delta del Paraná, Río Cabo, *Burkart 5119* (BAA). CÓRDOBA: Sierra Grande, Copina, *Hunziker 11439* (CORD, MO). Sierra Achala, *Hieronymus 335* (P).

Oenothera ravenii subsp. *argentinae* is a complex heterozygote which can be distinguished from the chromosomally homozygous subsp. *ravenii* only by its smaller flowers. The plants of subsp. *argentinae* seem more vigorous in growth than those of subsp. *ravenii* and may eventually replace them. Populations of subsp. *argentinae* that occur within the area of subsp. *ravenii* have, as a rule, larger flowers than those which occur beyond this area, in the Province of Buenos Aires. Populations of subsp. *argentinae* probably represent an early phase in the stabilization of their complex heterozygosity.

16c. **Oenothera ravenii** subsp. **chilensis** Dietrich, subsp. nov.—FIGS. 47–49, 127.

Folia rosulae anguste oblanceolata vel oblanceolata. Tubus floralis 2–3.5 cm longus. Gemmae ambito oblongae, 1.5–2 cm longae, 5–6 mm crassae, junctura sepalorum tubo florali rubro-fasciatae. Sepala immaculata; apices sepalorum 1.5–2 mm longi. Petala 2–2.5 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.2–2 cm longum. Semina 1.3–1.5 mm longa, 0.5–0.6 mm crassa, ambito late elliptica. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Rosette leaves narrowly oblanceolate to oblanceolate. Floral tube 2–3.5 cm long. Buds oblong in outline, 1.5–2 cm long, 5–6 mm thick, red at the junction of the sepals with the floral tube. Sepals not red-flecked; apices of the sepals 1.5–2 mm long. Petals 2–2.5 cm long. Anthers 6–8 mm long. Filaments 8–13 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 3–5 cm long. Stigma lobes 4–7 mm long. Ovary 1.2–2 cm long. Seeds 1.3–1.5 mm long, 0.5–0.6 mm thick, broadly elliptic in outline. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–February.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 24 July 1973. Source: Chile, Prov. Cautín, Molco at Lago Villarica, 1960, *W. Stubbe* (MO-2155707, holotype; CTES, DUSS, M, MO, isotypes).

Distribution (Fig. 226): In Chile from the provinces of Valdívia to Valparaíso.

Specimens examined from cultivated plants:

CHILE. CAUTÍN: Fundo Doyín near Loncoche, *Stubbe in 1960** (CTES, DUSS, M, MO). Molco at Lago Villarica, *Koch in 1961* (DUSS); *Stubbe in 1960** (DUSS, M, MO).

Additional specimens examined:

CHILE. VALPARAÍSO: Valparaíso, *Buchtien in 1895* (US). CONCEPCIÓN: At km 15 between Concepción and Coronel, *Cea & Ugarte in 1967* (CONC-35028). At km 42 between Concepción and Bulnes, *Villarroel & Weldt 119* (CONC). Near Concepción, *Macrae in 1825* (G, NY). MALLECO: Fundo San Elias near Victoria, 300 m, *Sparre 3315* (S). VALDIVIA: Panguipulli, 230 m, *Hollermayer 562* (M). Quinchilca, *Hollermayer 65a* (LP).

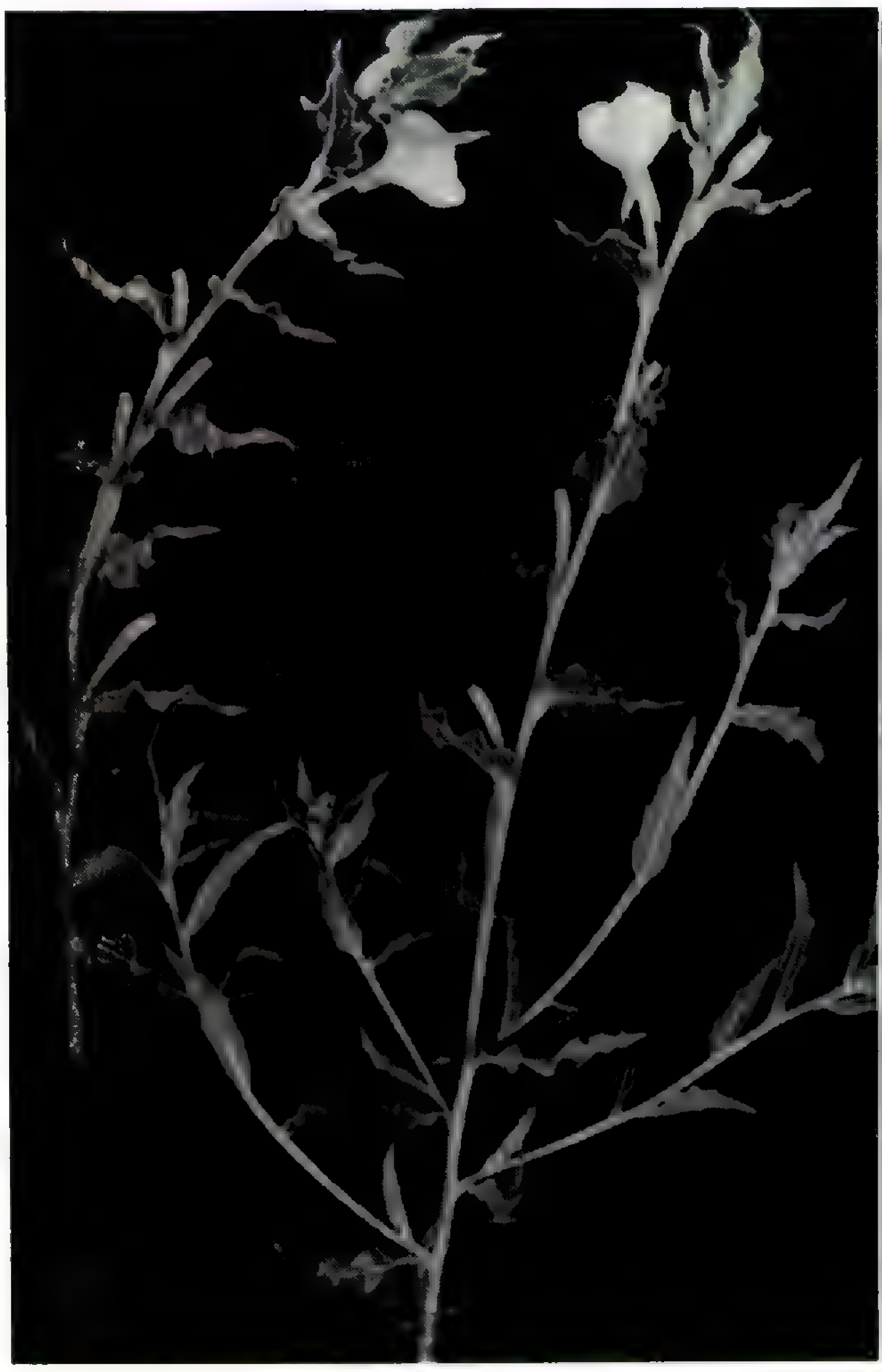
Oenothera ravenii subsp. *chilensis* can be distinguished from both other subspecies by its medium-sized flowers, buds oblong in outline, and consistently

oblanceolate leaves. It apparently arose from Chilean populations of the complex heterozygote *O. stricta* subsp. *stricta* by the segregation of two genomes originally derived from subsp. *ravenii* and the reconstitution of a chromosomally homozygous series of populations west of the Andes. In cultivated plants the influence of *O. odorata* on *O. ravenii* subsp. *chilensis* can be seen, especially in the form of the rosette leaves. This influence has come about because of crossing-over between the *ravenii*-genome and the *odorata*-genome within the complex heterozygote *O. stricta* subsp. *stricta*. The genomes of *O. ravenii* that segregated from *O. stricta* subsp. *stricta* apparently were modified in this way, and the resulting populations, although primarily *O. ravenii*, show the influence of *O. odorata*. In a similar manner, *O. affinis* seems to have modified Paraguayan populations of *O. ravenii* subsp. *ravenii*.

17. **Oenothera longiflora** L., Mant. Pl. 227. 1771.—Figs. 50–52, 55–57, 128–129, 177, 213–214.

Erect annual or biennial herb, forming a rosette, unbranched or with a branched main stem and widely arcuately ascending side branches arising from the rosette, 4–8 dm tall. Entire plant densely long-villous and sparsely glandular-pubescent. Rosette leaves narrowly elliptic to elliptic or oblanceolate to narrowly obovate, short-acute, gradually narrowed to a short petiole or sessile, cuneate at the base, 6–18 cm long, 1.5–3.5 cm wide; cauline leaves oblong to elliptic or narrowly ovate to ovate, short-acute, truncate to subcordate at the base, sessile, 1.5–6 cm long, 1–3 cm wide; bracts oblong to broadly oblong or ovate, short-acute or subobtuse, truncate to subcordate at the base, sessile, those of the central and upper portions of the inflorescence much shorter than the capsule they subtend, 1–3 cm long, 1–3 cm wide; leaves mostly irregularly serrate, the teeth blunt or acute, plane or undulate along the margins; bracts usually red along the margins. Inflorescence branched. Floral tube (6.5–)8–10 cm long, often streaked and flecked with dark red. Buds narrowly oblong to lanceolate in outline, red at the junction of the sepals with the floral tube, 2–3.5 cm long, 5–11 mm thick. Sepals green to yellowish green, often streaked and flecked with red; apices of the sepals erect or divergent, 1–3 mm long. Petals very broadly obovate, yellow, often with a red spot at the base, 2–4 cm long. Anthers 7–13 mm long. Filaments 14–24 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, or the style long, the stigma held above the anthers at anthesis, 8–13 cm long. Stigma lobes 6–12 mm long. Ovary 1.7–2 cm long. Capsule mostly curved and with 4 clearly distinct crenate valves at the apex, 3–4.5 cm long, 3–4 mm thick. Seeds elliptic to broadly elliptic, brown, 1.5–2 mm long, 0.8–1.1 mm thick. Self-compatible; self-pollinating and complex heterozygote. Gametic chromosome number, $n = 7$ (7 bivalents, ring of 14 or ring of 12 and 1 bivalent at meiotic metaphase I). Flowering time: October–March.

Type: Cultivated at Uppsala, Sweden, the seeds from the vicinity of Buenos Aires, Argentina, grown in 1752 or earlier, *C. Linnaeus* (LINN, holotype, POM photograph).



FIGURES 154–155. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—154. *O. grisea* (Chile, Valparaíso, Las Ventanas, *Constance in 1965*).—155. *O. nocturna* (Peru, Lima, *Santarius 2333*).

Distribution (Figs. 229–230): In Brazil only in Rio Grande do Sul; in Uruguay in the departments of Río Negro, Colonia, San José, and Montevideo; and in Argentina in the provinces of Corrientes, Entre Ríos, and Buenos Aires.

Oenothera longiflora is unmistakable because of its dense long-villous pubescence and long floral tube. It is characteristic of sandy places along rivers and near the coast. This species is related to *O. ravenii*, as shown by similarities in habit, short bracts, reddish leaf margins, and the red basal spot on each petal. The seeds of *O. longiflora* are the largest in the series.

Oenothera longiflora subsp. *grandiflora* is chromosomally homozygous, subsp. *longiflora* is chromosomally heterozygous. The latter has two complexes from subsp. *grandiflora*, but one of them appears to have been influenced by introgression from *O. ravenii*. Among the F_1 progeny derived from crossing the heterozygote *O. longiflora* subsp. *longiflora* with *O. ravenii*, there are two classes of progeny, one intermediate and the other more similar to *O. ravenii*. The influence of the "pure" *O. longiflora* subsp. *grandiflora* genome upon the characteristics of *O. longiflora* subsp. *longiflora* is so strong, however, that it seems undesirable to recognize this particular complex heterozygote as a species separate from subsp. *grandiflora*.

Oenothera longiflora subsp. *grandiflora* is evidently very rare and occurs

only at scattered localities. It may either have a relictual distribution, therefore, or be derived as a viable homozygous segregate from the chromosomally structurally heterozygous subsp. *longiflora.*

Key to the Subspecies

1. Style long, the stigma held above the anthers at anthesis; buds 2.5–3.5 cm long; petals 3–4 cm long .... 17a. subsp. *grandiflora*
1'. Style short, the anthers shedding pollen directly on the stigma at anthesis; buds 2–2.5 cm long; petals 2–3 cm long .... 17b. subsp. *longiflora*

17a. **Oenothera longiflora** subsp. **grandiflora** Dietrich, subsp. nov.—Figs. 50–52, 128, 177, 213.

Folia rosulae 2.5–3.5 cm lata; folia caulina 2–3 cm lata; bractea 1.5–2 cm lata, 1.5–2.5 cm longa. Gemmae 2.5–3.5 cm longae, 8–11 mm crassae; apices sepalorum divergentes, ca. 3 mm longi. Petala 3–4 cm longa, basi rubro-maculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Rosette leaves 2.5–3.5 cm wide; cauline leaves 2–3 cm wide; bracts 1.5–2 cm wide, 1.5–2.5 cm long. Buds 2.5–3.5 cm long, 8–11 mm thick; apices of the sepals divergent, ca. 3 mm long. Petals 3–4 cm long, with a red spot at the base of each one. Anthers 10–13 mm long. Filaments 22–24 mm long. Stigma lobes 8–12 mm long. Style long, the stigma elevated above the anthers at anthesis. Self-compatible. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 19 Oct. 1972. Source: Argentina, Prov. Corrientes, Paso de los Libres, 27 Mar. 1964, *A. Krapovickas & C. Cristóbal 11293* (MO-2155211, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 229): Known only from the type locality and one locality in the province of Entre Ríos, Argentina.

Specimen examined from cultivated plants:

Argentina. corrientes: Paso de los Libres, *Krapovickas & Cristóbal 11293* (DUSS, M, MO).

Additional specimens examined:

Argentina. entre ríos: Dep Federación, Santa Ana at Río Uruguay, *Burkart 29273, 26317* (SI).

In 1962 and 1963 there appeared in Düsseldorf among the progeny of plants growing wild in the Botanical Garden of Buenos Aires (*Göpel in 1961*), one plant with 7 bivalents and another with a ring of 4 and 5 bivalents. Unfortunately, both of these strains were lost, since a test-progeny grown in 1973 yielded only plants with a ring of 12 and 1 bivalent which would therefore be referred to *O. longiflora* subsp. *longiflora.*

17b. **Oenothera longiflora** subsp. **longiflora**.—Figs. 55–57, 129, 214.

Onagra pellucida Moench, Meth. Pl. 1: 675. 1794. type: The herbarium of Moench apparently no longer exists.

Onothera polymorpha H. Lév. race *longiflora* (L.) H. Lév., Mongr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 324. 1909.

FIGURES 156–159. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—156. *O. magellanica* (Argentina, Mendoza, *Santarius 1581*).—157. *O. villaricae* (Chile, Cautín, *Göpel in 1961*).—158. *O. hechtii* (Argentina, Tucumán, *Hecht 1964-81*).—159. *O. elongata* (Bolivia, Tarija, *Santarius 1956*).

O. polymorpha race *longiflora* var. *sellowii* Link & Otto ex H. Lév., Monogr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 324. 1909. LECTOTYPE: Cape Verde Islands, Brava, mountains, 900 m, 30 Mar. 1864, *R. T. Lowe* (BM; P, isolectotype). Locality given in error as being in Bolivia by H. Léveillé.

Oenothera mollissima L. var. *longiflora* (L.) Hassler, Bull. Soc. Bot. Genève, sér. 2, 5: 274. 1913.

Raimannia longiflora (L.) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.

Rosette leaves 1.5–2.5 cm wide; cauline leaves 1.5–2.5 cm wide; bracts 1–1.5 cm long, 1–1.5 cm wide. Buds 2–2.5 cm long; apices of the sepals erect, 1–2 mm long. Petals 2–3 cm long, often with a red spot at the base of each one. Anthers 7–12 mm long. Filaments 14–22 mm long. Stigma lobes 6–8 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 12 and 1 bivalent** at meiotic metaphase I).

Distribution (Fig. 230): In Brazil only in Rio Grande do Sul; in Uruguay in the departments of Río Negro, Colonia, San José, and Montevideo; and in Argentina in the provinces of Entre Ríos and Buenos Aires. Not known from the province of Corrientes in Argentina, where *O. longiflora* subsp. *grandiflora* occurs.

Specimens examined from cultivated plants:

URUGUAY. COLONIA: Sandy places at the northern entrance of Juan L. Lacaze, *Santarius 73*, 74*, 77, 79, 80, 81*, 82–84, 86,* 87, 88,* 89, 90* (DUSS; 81 also CTES; *73, 81* also M; *73, 81, 89* also MO). Dunes NW of Juan L. Lacaze, *Santarius 109–115, 116** (DUSS; *116* also M; *109, 116* also MO).

ARGENTINA. BUENOS AIRES: Wild in the Botanical Garden of Buenos Aires, *Göpel in 1961*** (DUSS, M). La Plata, *Hecht 1964-22** (CTES, DUSS, M). Villa Ortuzor in Buenos Aires, *Hecht 1964-123* (DUSS, M).

Additional specimens examined:

BRAZIL. RIO GRANDE DO SUL: Rio Grande, *Gaudichaud 1287* (P).

URUGUAY. RÍO NEGRO: San Javier, *Puerto 8415* (MVFA); *Herter 82853* (POM). COLONIA: Colonia, *Molfino 31-1650* (POM); *N.N. 27* (BAA). Dunes near Riachuelo, *Cabrera 3856, 3345* (LP). SAN JOSÉ: Arazati, *Arrillaga 641* (MVFA). Playa Pascual, *Arrillaga 741* (MVFA). MONTEVIDEO: Montevideo, *Fruchard in 1874* (RSA); *Barattini in 1939* (MO); *N.N.* (MPU); *Lorentz 307* (G). Sta. Lucía, *Fruchard in 1874* (US); *Fruchard in 1875* (P). Coast near Montevideo, *Gibert 339* (K). Maluni, *Rosa-Mato 1525* (LIL). Punta Gorda, *Osten 4664* (G), *22709a* (GH). Between La Colorada and Pajas Blancas, *Lema 6458* (F, MVFA). Miguelete, *Berro 5340* (MVFA). Cerro, *Herter 162* (F, G, GH, HBG, LE, M, MO, POM, S, Z). Buceo, *Felippone 2895, 5971* (SI). Carrasco, *Fruchard in 1875* (P); *Osten 5784* (CORD, US); *Felippone 6097* (SI); *Legrand 343* (POM); *Rosengurtt B418* (POM). Malvín, *Felippone 3342* (SI). ROCHA: Eastern coast, *Tweedie 78* (BM).

ARGENTINA. BUENOS AIRES: Dock Sur, *Hicken 784* (LIL, SI); *Molfino 221* (POM). Pellegrini, *Cabrera 6954* (LP, NY). Devoto, *Hirschborn 40* (POM). Maciel, *Molfino 25842* (SP). La Plata, *Hirschborn 676* (POM). Paternal, *Parodi 8993* (GH, K, POM). Carón, *Franqueville* (P). ENTRE RÍOS: Concepción del Uruguay, *Lorentz 1230* (CORD, G, SI). Concordia, *Spegazzini 88* (BAB). Santa Ana, *Gamerro 1310* (LP). Berduc, *Crovetto & Piccinini 4654* (BAB). El Palmar, *Pedelaborde in 1940* (SI). Between Gómez and Emb. Ferrari near Concordia, *Meyer 10974* (LIL).

Specimens from outside of South America (naturalized):

FRANCE. Near Bayonne, *Lange in 1851* (P); *Bordère in 1877* (G); *Blanchet in 1880* (P). Between Bayonne and Boucau, 1881, *Blanchet 70* (LISU, LY, MPU, P); *Neyraut in 1889* (COI, MPU); 1933, *Hibon 1461-2* (P). Boucau, *Deflers in 1879* (MPU); *Neyraut in 1902* (LY); *Willkomm* (COI). Dep. Landes, Rivière, *Foucaud in 1881, in 1882* (LY). Biarritz, *Henry in 1903* (B). Anglet, *Neyraut in 1905* (MPU).

PORTUGAL. Açôres, Fayal, *Donat in 1868* (G, P). MADEIRA: Serro de S. Roque, 1865–

1866, *Mandon 441* (G, P). Mountains above the Povoação, *N.N. 766, 768* (K); *Lowe in 1866* (BM).

Spain. canary islands: Puerto de La Orotava, *N.N. 2352* (K).

South Africa. cape: Camps Bay, *BS. in 1846* (K); *Prior in 1846* (PRE). Wellington, *Thomson in 1881* (PRE). Cape of Good Hope, *Pappe* (K).

Australia. new south wales: Raymond Terrace, *Coans in 1961* (NSW-65372). Princess Highway at crossing of Minimurra River, 1 mi S of Albion Park, *Raven et al. 25895 in 1970* (MO, NSW); *Briggs 3950 in 1970* (NSW).

Hybrids with *O. stricta* subsp. *stricta* have been collected in France, where both species grow together near Biarritz: Biarritz, *Cornuault in 1907* (MPU). Anglet, 1947, *Jallu 5257* (LD), 1964, *7832* (LISE).

Early specimens from plants cultivated in Botanical Gardens:

Erlangen, Germany, Herb. *Schreber in 1779* (M). Paris, *in 1781* (MPU). Erlangen, Herb. *Schreber in 1800* (M). Halle, Germany, *Fischer in 1801* (L). Montpellier, France, *in 1808* (MPU). Hamburg, Germany, from seeds of the Botanical Garden Kiel, *in 1815* (HBG). Munich, Germany, Herb. *Zuccarini in 1835* (M; as *O. nervosa*). Paris, *Abbé Pouret in 1847* (P). Hort. Cantab., seeds from the Canary Islands, Herb. *Gray in 1867* (GH; as *O. canariensis*).

Oenothera longiflora reported in literature from outside of South America:

France: Gandoger (1886: 49); Rouy & Camus (1901: 201); Coste (1903: 81); Thellung (1912); Bonnier (1921: 29); Fournier (1937: 598); Issler, et al. (1965: 357); Raven (1968).

Belgium: Jean (1975).

Portugal: Gandoger (1886: 49); Coutinho (1913: 427; 1939: 508); Raven (1968).

Azores: Trelease (1897: 114).

Madeira: Lowe (1868: 275); Menezes (1914: 71).

Spain: Raven (1968).

South Africa: Phillips (1917: 99; as *O. villosa*); Adamson & Salter (1950: 606).

Jamaica: Grisebach (1860: 273).

18. **Oenothera catharinensis** Cambess., in St.-Hilaire, Fl. Bras. Mer. 2: 270. 1829.—Figs. 3, 53–54, 130.

O. mollissima sensu Munz, Amer. J. Bot. 22: 659. 1935, pro parte.

Erect annual herb, not forming a rosette, bushily branched near the base, 1–5 dm tall. Plants densely to sparsely strigillose and villous in the lower portions, densely to sparsely long-villous and thickly to sparsely glandular-pubescent elsewhere. Cauline leaves cultrate to narrowly lanceolate, acute, acute to rounded at the base, sessile, 3–5 cm long, 0.7–1 cm wide; bracts narrowly oblong to lanceolate, acute to rounded at the base, sessile, 2–4 cm long, 0.5–0.8 cm wide, mostly shorter than the capsules they subtend; leaves plane and irregularly serrate with blunt teeth. Inflorescence branched. Floral tube 3–4 cm long. Buds lanceolate in outline, 1.8–2.2 cm long, 5–6 mm thick, green or yellowish green; apices of the sepals erect, ca. 1.5 mm long. Petals very broadly obovate, retuse, 3–3.5 cm long. Anthers 7–10 mm long. Filaments 15–18 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 4–5.5 cm long. Stigma lobes 5–8 mm long. Ovary 1–1.5 cm long. Capsule 3–4 cm long, 3–4 mm thick. Seeds elliptic in outline, 1.5–1.8 mm long, 0.6–0.8 mm wide, brown. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 14** or ring of 4 and 5 bivalents*** at meiotic metaphase I). Flowering time: October–March.

Type: Brazil, Santa Catarina, Îlha Santa Catarina, Apr. (1816–1821), *Auguste de St.-Hilaire 1721* (P, holotype, F and GH photographs; MPU, P, isotypes).

Distribution (Fig. 229): Apparently only along the coast of the state of Santa Catarina, Brazil.

Specimens examined from cultivated plants:

BRAZIL. SANTA CATARINA: Coast near Itapema, *Hatschbach in 1971*** (DUSS, M, MO). Isle of Santa Catarina, Praias Inglese, *Conrad & Dietrich 8****, *9**, *10**, *13** (DUSS).

Additional specimens examined:

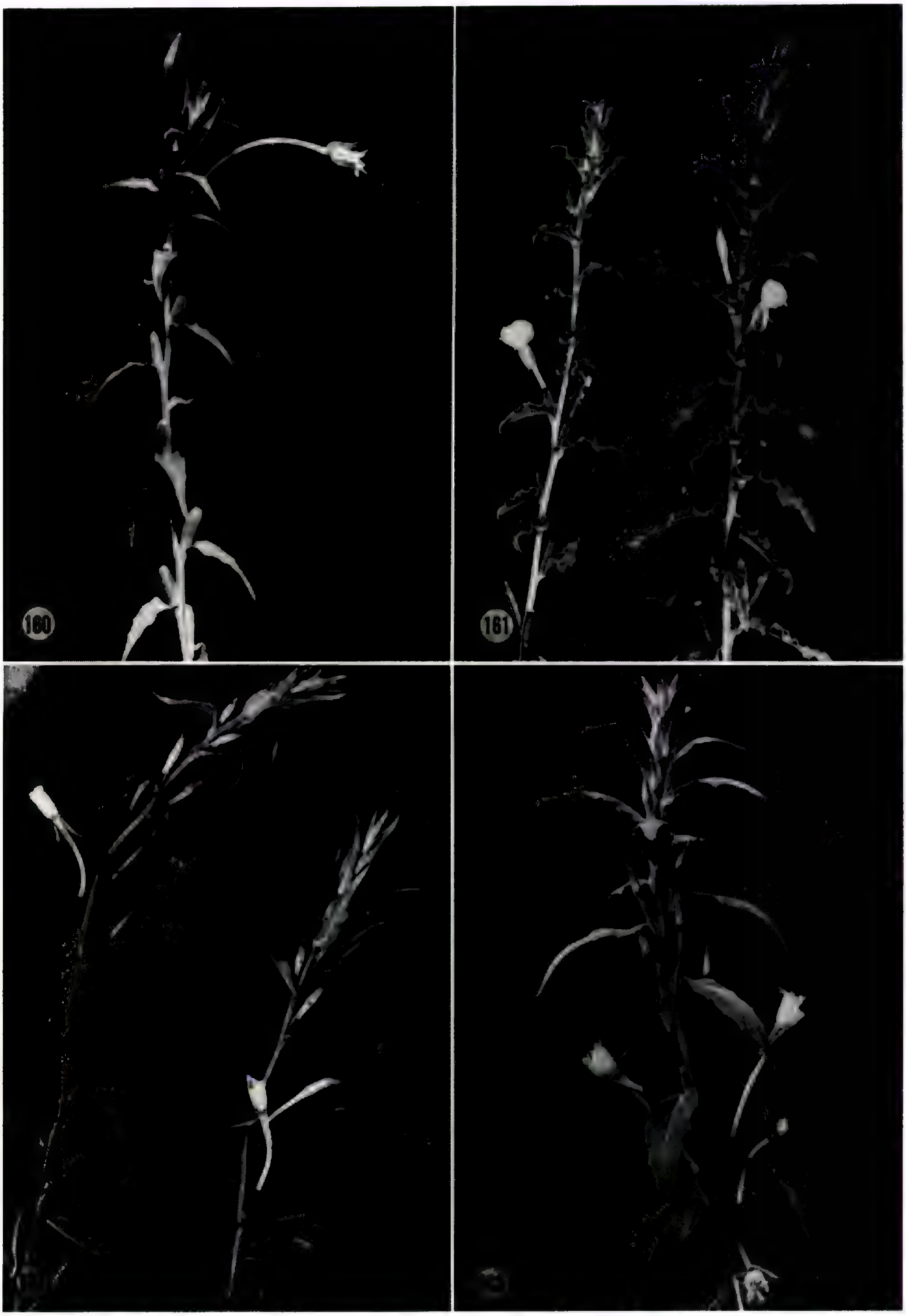
BRAZIL. SANTA CATARINA: Santa Catarina, *N.N.* (GOET). Isle of Santa Catarina, *Gaudichaud 252* (P). Isle of Santa Catarina, Pântano do Sul, *Klein et al. 5824* (HBR, RSA). Rio Vermelho, *Klein et al. 5801* (HBR, RSA); *Perdonnet 233* (G). Laguna, *Reitz & Klein 185* (RSA), *137* (HBR, RSA).

Oenothera catharinensis has generally been regarded as a synonym of the complex structural heterozygote *O. mollissima* (Munz, 1935), but it can be distinguished from that species by its strigillose pubescence, which is never present in *O. mollissima*, and its larger flowers. The pubescence, flower size, and short bracts of *O. catharinensis* indicate that it is a relative of *O. ravenii* rather than of *O. mollissima*.

I have been unable to discover any evidence that *O. catharinensis* has participated in the origin of any complex heterozygote. From this, I conclude that it may be a species of relatively recent origin derived from an ancestor similar to *O. ravenii* as an obligate annual strain with altered characteristics (Fig. 8). The occurrence of complex heterozygote strains with a ring of 14 chromosomes may reflect a situation similar to that in *O. affinis* and *O. odorata*.

19. **Oenothera indecora** Cambess. in St.-Hilaire, Fl. Bras. Mer. 2: 268. 1729.—FIGS. 2, 44–46, 131–132, 178–179, 215–217.

Erect annual, forming a rosette, unbranched or with a moderately or strongly branched main stem and arcuate to obliquely ascending side branches arising from the rosette, 2–6 dm tall. Entire plant sparsely long-villous with erect hairs, densely to sparsely short-villous, and densely glandular-pubescent; or only densely short-villous and densely glandular-pubescent. Rosette leaves narrowly oblanceolate, acute, gradually or ± abruptly narrowed to the petiole, 4–8 cm long, 0.2–1.3 cm wide; cauline leaves very narrowly elliptic to lanceolate, acute, acute at the base, sessile, 2.5–7 cm long, 0.2–1.2 cm wide; bracts very narrowly elliptic to elliptic, acute, acute at the base, sessile, longer than or about the same length as the capsules they subtend, 1.5–5 cm long, 0.2–1 cm wide; leaves plane or undulate at the margins, irregularly serrate with blunt teeth. Inflorescence branched. Floral tube 0.5–1.5 cm long. Buds oblong to broadly elliptic in outline, 0.2–0.8 cm long, 1.5–4 mm thick. Sepals green or yellowish green, often ± densely flecked with reddish brown; apices of the sepals 0.5–1 mm long, erect. Petals broadly elliptic to very broadly obovate, yellow or bright yellow, 4–10 mm long. Anthers 1.5–4 mm long. Filaments 1.5–7 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1–2 cm long. Stigma lobes 1–2 mm long. Ovary 1–1.5 cm long. Capsule 2–3 cm long, 1.5–2 mm thick. Seeds broadly elliptic to rotund in outline, 0.7–1.3 mm long, 0.3–0.5 mm thick. Cleistogamous, almost always fertilized in bud. Gametic chromosome number, $n = 7$ (7 bivalents or ring of 14 at meiotic metaphase I).



FIGURES 160–163. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—160. *O. pseudoelongata* (Bolivia, Cochabamba, *Santarius 1988*).—161. *O. cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—162. *O. siambonensis* (Argentina, Tucumán, *Göpel in 1961*).—163. *O. brevipetala* (Bolivia, Cochabamba, *Santarius 1972*).

Type: Brazil, Rio Grande do Sul, sandy places near the farm Manguiera, not far from the city of Rio Grande, Aug. (1816–1821), *Auguste de St. Hilaire 1872 bis* (P, holotype, F and GH photographs; MPU, P, isotypes).

Distribution (Fig. 231, 233): In Brazil from the states of São Paulo to Rio Grande do Sul; in Uruguay in the departments of Cerro Largo, Treinta y Tres, Rocha, Maldonado, Montevideo, San José, Ártigas, Riviera, Salto, and Río Negro; in Argentina throughout the northern and eastern portions of the republic, in the provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, Formosa, Chaco, Santiago del Estero, Santa Fé, Córdoba, San Luis, Misiones, Corrientes, Entre Ríos, and Buenos Aires; in central Paraguay; and in Bolivia in the vicinity of La Paz (subsp. *boliviensis*).

Together with *O. mendocinensis* and *O. verrucosa*, *O. indecora* contradicts the rule that chromosomally homozygous entities in the genus are usually large-flowered. In comparison with *O. mendocinensis*, *O. indecora* has wider leaves, shorter capsules, smaller seeds, and never any strigillose pubescence.

Key to the Subspecies

1. Plants exclusively short villous and glandular-pubescent, appearing glabrous to the naked eye.
   2. Bracts 0.5–1.3 cm wide; buds 4–8 mm long; petals 0.5–1 cm long .... 19b. subsp. *bonariensis*
   2′. Bracts 1.5–2 mm wide; buds 2–3 mm long; petals 0.2–0.3 cm long .... 19c. subsp. *boliviensis*

1′. Plants sparsely long villous, densely short villous, and densely glandular-pubescent, appearing pubescent to the naked eye; bracts 0.5–1 cm wide; buds 3–8 mm long; petals 0.4–1 cm long .... 19a. subsp. *indecora*

19a. **Oenothera indecora** subsp. **indecora**.—Figs. 131, 178, 215–216.

Onothera polymorpha H. Lév. race *mollissima* (L.) H. Lév. var. *indecora* (Cambess.) H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909.
Raimannia indecora (Cambess.) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.
Oenothera argentinae H. Lév. & Thell. var. *longipila* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherlands, Weert, oatfield near the Karelke meal factory, 13 Aug. 1920, *A. W. Kloos* (L-95264486; BAS, isolectotype).

Plants 2–4 dm tall. Entire plant sparsely long-villous, densely short-villous, and densely glandular-pubescent. Rosette leaves and cauline leaves 5–7 cm long, 0.5–1 cm wide; bracts 3–5 cm long, 0.5–1 cm wide. Buds 0.3–0.8 cm long, 2.5–4 mm thick. Sepals ± densely flecked with reddish brown, seldom immaculate. Petals 0.4–1 cm long. Anthers 2–3 mm long. Filaments 3–6 mm long. Seeds elliptic in outline, 1–1.3 mm long, 0.4–0.5 mm thick. Cleistogamous. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: Brazil, September–July; Uruguay, Paraguay and Argentina, September–May.

Distribution (Fig. 231): In Brazil from the states of São Paulo to Rio Grande do Sul; prevalent in the coastal departments of Cerro Largo, Treinta y Tres, Rocha, Maldonado, Montevideo, Colonia, Canelones and San José in Uruguay, and also in the departments of Ártigas, Salto, Lavalleja and Rivera; in Argentina known from the provinces of Misiones, Corrientes, Entre Ríos, For-

mosa, Chaco and Córdoba; in Paraguay only from Encarnación in the southeast of the country.

Specimens examined from cultivated plants:

URUGUAY. MALDONADO: Sandy places in the southern part of Piriapolis, *Santarius 147, 150*, 151, 152, 153*, 155, 156* (DUSS; *150* also CTES; *150, 152* also M, MO). FLORIDA: At the railroad 1–3 km NE and SW of Mansavillagra, *Santarius 205*, 206*, 208*, 209*, 212*, 213** (DUSS; *205, 208, 209* also CTES, M; *205, 206, 208, 209* also MO). Lavadero San Pedro, *Hecht 1964-63** (DUSS, M, MO).

Additional specimens examined:

BRAZIL. SÃO PAULO: Pinheiros, *Gehrt 34390* (POM, SP). PARANÁ: Curitiba, *Hoehne 23080* (POM, SP). Pôrto Vitória near Curitiba, *Hatschbach 1-1969* (UC). SANTA CATARINA: Itajai, *Klein 2567, 2686* (HBR, RSA); *Mueller s.n.* (R), *397* (K). Near Palmitos, 400 m, *Smith & Reitz 12584* (HBR, US). Rio Irani 12 km S of Faxinal des Guedes, 500–600 m, *Smith & Klein 12903* (HBR, RSA). Rio Uruguai near Itapiranga, 200 m, *Smith & Klein 13184* (HBR, RSA). Ilha de Santa Catarina, *Klein & Bresolin 8338* (HBR). Araranguá near Sombrio, *Reitz C748* (BR, HBR). Pirão Frio near Sombrio, 10 m, *Reitz & Klein 9072* (HBR). Est. Exp. de Videira, *Santos 2894* (R). Tubarão near Laguna, *Ule 1256* (HBG, P). RIO GRANDE DO SUL: Near Trés de Maio, *Santos 2763* (R). Serro de Pustral near Sta. Maria, *Vidal 01199* (R). Palmeira near Xingu, 650 m, *Bornmüller 745* (GH). São Sepé near Cacapava, *Rosengurtt 8734* (MVFA). City of Rio Grande, *Malme 270* (S). Viera, *Archer 36795* (SP), *4301* (BR, GH, NY, POM, US). Between Pelotas and Rio Grande, *Krapovickas & Cristóbal 22901* (MO). Pelotas, *da Costa Sacco 1116* (F, HBR); *Casagrand et al. 13* (CTES). Facenda Saledade near Rio Pardo, *Jürgens 25, 97* (B); *Vidal 01526, 01533* (R). Montenegro near L. S. Pedro, *Sehnem 3833* (B, SI). San Leopoldo, *Reuter in 1953* (R); *Eugenio 201, 206* (NY); *Rambo 293* (LIL). Uruguayana, *Palacios & Cuezzo 202, 227* (LIL); *Vidal 01315, 01318* (R). Passo de Ricarde at Rio Piratini, *Pereira 6773* (RB). Toca do Tigre near Itapoan, *Rambo 48931* (LIL, MO), *48934* (HBR, RSA). Pôrto Alegre, *Rambo 293* (SP). Gloria near Pôrto Alegre, *Rambo 978* (SP), *27196* (LIL, S), *28995* (RSA, LIL). Villa Manresa near Pôrto Alegre, *Rambo 37466* (F, HBR, LIL, RSA), *57073* (HBR), *55570* (B, HBR). Balneario Ipanema near Pôrto Alegre, *Emrich 1126* (LIL). São João near Pôrto Alegre, *Reineck & Czermak 30* (HBG). Praia Tramandahy near Pôrto Alegre, *Vidal in 1913* (R). Montenegro, *Rambo 29702* (LIL). Pareci near Montenegro, *Rambo 29702, 42445* (LIL). Amaral Ribeiro near Taquara, *Rambo 42391* (F, LIL). Travessão near Hamburgo, *Rambo 42181* (LIL). Osorio, *Rambo 48887* (LIL). Morro Sapucaia near Pôrto Alegre, *Rambo 37381* (SI). Est. Azevedo, *Rambo 43276* (LIL).

URUGUAY. ÁRTIGAS: Cuareim, *Berro 2319* (MVFA). Santa Amaro, *Jürgens 168* (B). SALTO: Dayman, *Osten 5258* (SI, US). RIVERA: Cuñapiru, 200–230 m, *Wright in 1928* (BM). FLORIDA: Mansavillagra, *Rosengurtt B790* (POM). SAN JOSÉ: Sierra Mahoma, *Izaguirre 2591* (MVFA). Rincón del Pino, *Izaguirre 9543* (MVFA). COLONIA: Between Colonia and Montevideo, *Burkart 29012* (SI). MONTEVIDEO: Carrasco, *Rosengurtt 861* (POM); *Berro 7550* (MVFA). Sta. Lucía, *Fruchard 788* (P). CERRO LARGO: Est. Perdomo near Ruta 8 and Arroyo Tacuari, *Arrillaga 2358* (F). Between Río Negro and Acegua, *Rosengurtt 851a* (POM). TREINTA Y TRES: Km 323 at Ruta 8, *Marchesi 2268* (MVFA). LAVALLEJA: La Lorenzita, *Lombardo 9132* (MVFA). Abra de Perdano, *Olano 8838* (MVFA). Cerro Arequita near Minas, *Krapovickas & Cristóbal 16149* (CTES). CANELONES: Sta. Lucía, *Gibert 988* (K); *Felippone 5574, 5589* (SI). ROCHA: La Coronilla, *Brescia 3984* (MVFA). Parque Sta. Tereza, *Rodriguez 8146* (MVFA). MALDONADO: Sierra de las Animas, *Izaguirre 10751* (MVFA). Cerro Pan de Azúcar, *Bartlett 21003* (GH, MICH, UC, US).

PARAGUAY. Encarnación, *Hassler 1476* (SI); *Bertoni 4532* (LIL).

ARGENTINA. MISIONES: Bonpland, *Van de Venne 275* (POM). Montecarlo, *Schinini 5493* (CTES). CORRIENTES: Dep. Mercedes, at Río Miriñay near Ruta 23, *Schinini et al. 7124* (CTES, MO). ENTRE RÍOS: Concepción del Uruguay, *Lorentz 424 pro parte* (GOET); *Burkart 28762* (MO). Between Colón and Concepción, *Burkart 28991* (MO). San Salvado, *Baez 52972* (BAB). Arroyo Maimol near Colón, *Nicora 3238* (LIL). Km 249 at Ruta 14 near Concrodia, *Burkart 22664* (MO). Arroyo Isletas, *Burkart 27034* (MO). Paraná, *Burkart 23759* (MO); *Anetto in 1891–92* (CORD). Gualeguaychi, *Meyer 10331* (LIL). Médanos, *Burkart 3470* (POM). Río Tale, *Schulz 284* (LIL). Paranacito, *Ragonese 6* (BAB). FORMOSA: *N.N. in 1904* (SI-4860). Reventón near Pilcomayo, *Morel 1913* (LIL). CHACO: Dep. Independencia, Campo Largo 8 km from J. Mármol, *Bacigalupo et al. 9601* (BAA, MO, SI), *9604* (BAA). Puerto El Colorado, *Rojas 12113* (LIL). Dep. Napalpi, C. del Bermejo, *Burotorich 535* (LIL).

CÓRDOBA: Vicinity of Alta Gracia, *Hunziker 7710* (CORD). Sierra Ochoa near Sta. María, *Stuckert 13562* (CORD). Between Est. Burmeister and Onagoity near Gral. S. Martín, *Di Fulvio 21411* (CORD). At km 571 of Ruta 35 between Huinca Renancó and Río Quinto, *Hunziker & Di Fulvio 21430* (CORD). Near Copina, *Hunziker 6951* (CORD).

Specimens from outside of South America:

NETHERLANDS. Wormerveer, meal factory, *Jansen & Kloos in 1913* (BAS).

FRANCE. Dép. Nord, Dunkerque, *Bouly de Lesdain in 1924* (BAS).

HUNGARY. Györ at river Danube, 1916, *Polgar 2468* (BAS).

Plants intermediate between *O. indecora* subsp. *indecora* and *O. indecora* subsp. *bonariensis* are occasional in the zone of overlap between these two entities and may be recognized by the fact that they are only sparsely long villous. All plants of this species are in effect cleistogamous, fertilization taking place in bud well before the unfolding of the flowers; and this factor alone must drastically limit the possibility of hybridization and thus help to maintain the integrity of the two subspecies where they come together.

One of the genomes of the complex heterozygote *O. montevidensis* is derived from *O. indecora* subsp. *indecora.*

19b. **Oenothera indecora** subsp. **bonariensis** Dietrich, subsp. nov.—FIGS. 2, 44–46, 132, 179, 217.

Oenothera humifusa Torr. & A. Gray f. *erecta* Thell. & Zimmerm., Repert. Spec. Nov. Regni Veg. 14: 375. 1916. TYPE: Germany, port of Ludwigshafen, Sep. 1909, *F. Zimmermann* (BAS).

Onothera argentinae H. Lév. & Thell. ex H. Lév., Monde Pl., sér. 2, 18 (108): 52. 1917; H. Lév. & Thell., Repert. Spec. Nov. Regni Veg. 15: 133. 1918. LECTOTYPE: Germany, dockyard of Uerdingen at the Rhine near an oil refinery, 26 Sep. 1915, *Bonte* (Z; BA, POM, isolectotypes). Léveillé's mention of *Onothera argentinae* in Monde Pl., sér. 2, 18 (108): 52. 1917, is not a nomen nudum, as stated by Lauener (1972: 424).

O. argentinae var. *typica* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherlands, Rotterdam, Maashaven meal factory, 10 Sep. 1920, *A. W. Kloos* (L-954264523; BAS, isolectotype).

O. argentinae var. *brevipila* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. LECTOTYPE: Netherland, Weert, oatfield near the Karelke meal factory, 13 Aug. 1920, *A. W. Kloos* (L-954264489; BAS, isolectotype).

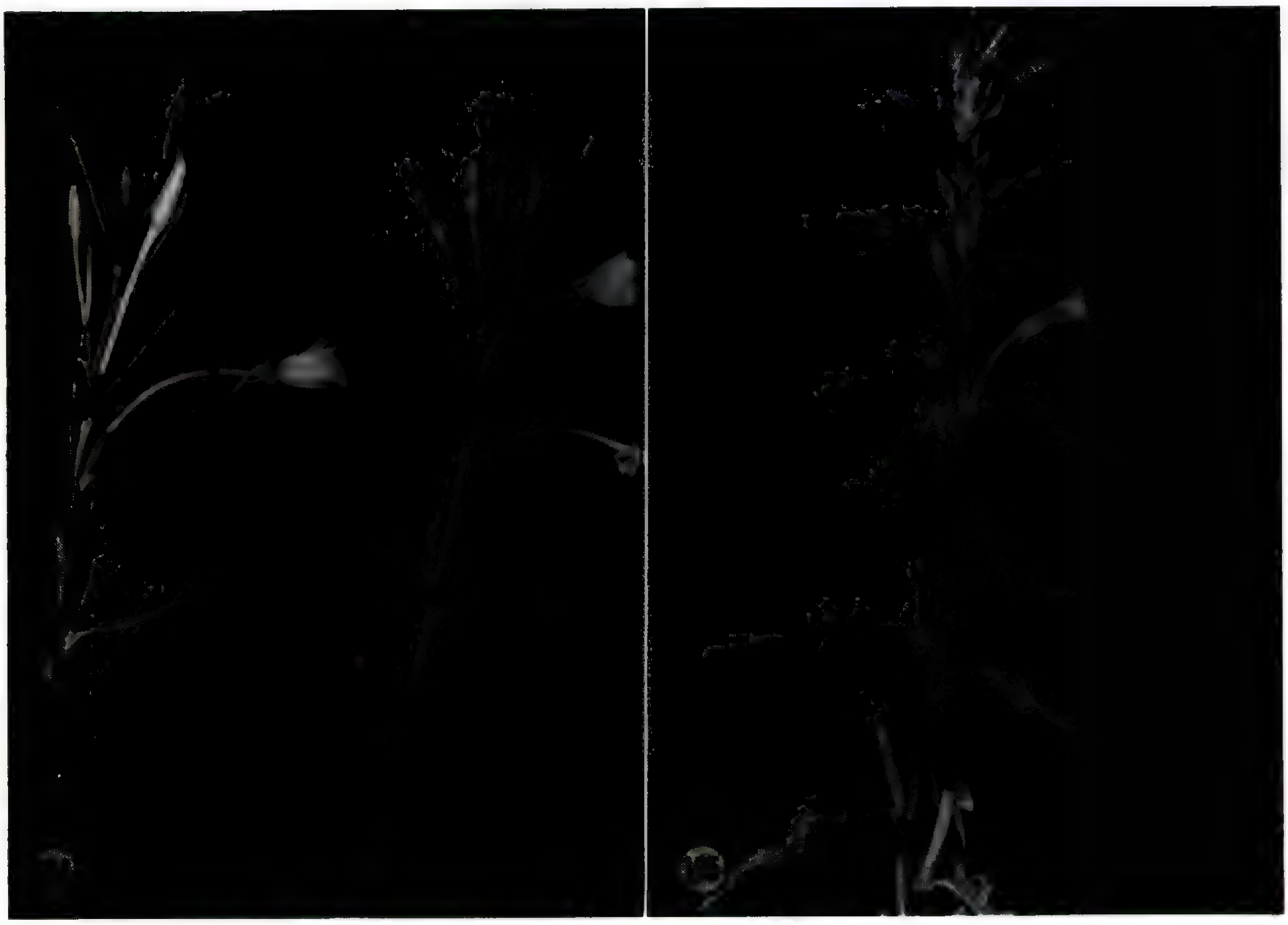
O. indecora sensu Munz, Physis 11: 281. 1933, pro parte; Amer. J. Bot. 22: 658. 1935, pro parte; sensu Munz, Fl. Brasílica 9(41): 53. 1947, pro parte.

O. argentinae "Erlangen" Haustein, Z. Indukt. Abstammungs- Vererbungsl. 84: 418. 1952.

O. indecora "Argentinae," "Buenos Aires" and "Reconquista" Cleland, Jap. J. Genet. 43: 332. 1968.

Plantae 2–6 dm altae, ubique dense breviter villosa denseque glanduloso-pubescentes, sine lente ut videtur glabrae. Folia rosulae 5–7 cm longa, 0.5–1.3 cm lata; bractea 3–5 cm longa, 0.5–1.3 cm lata. Gemmae 0.4–0.8 cm longae, 2.5–4 mm crassae. Sepala viridia vel flavovirentia, raro rubro. Semina ambito late elliptica, 0.7–1 mm longa, 0.4–0.5 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica vel heterozygotica complexa.

Plants 2–6 dm tall. Entire plant densely short-villous and densely glandular-pubescent, apparently glabrous when viewed without a lens. Rosette leaves 5–7 cm long, 0.5–1.3 cm wide; bracts 3–5 cm long, 0.5–1.3 cm wide. Buds 0.4–0.8 cm long, 2.5–4 mm thick. Sepals green or yellowish green, rarely flushed with red. Petals 0.5–1 cm long. Anthers 1.5–4 mm long. Filaments 4–7 mm long. Seeds broadly elliptic in outline, 0.7–1 mm long, 0.4–0.5 mm thick. Self-polli-



FIGURES 164–165. Taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—164. *O. acuticarpa* (Argentina, Tucumán, *Göpel in 1961*).—165. *O. tucumanensis* (Argentina, Tucumán, *Santarius 1657*).

nating and often cleistogamous. Gametic chromosome number, $n = 7$ (7 bivalents* or ring of 14** at meiotic metaphase I). Flowering time: September–July.

Type: Argentina, Prov. Buenos Aires, Isla Santiago near La Plata, 24 Nov. 1935, *A. L. Cabrera 3406* (NY, holotype; F, G, LIL, LP, POM, SI, UC, isotypes).

Distribution (Fig. 233): In Brazil from the state of São Paulo to Rio Grande do Sul; in Uruguay the stations are all in the western and southwestern departments of Río Negro, San José, and Florida; in central Paraguay and throughout the range of the species in Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: On sandy soil of Isla Santiago near La Plata, *Santarius 275**, *276**, *277**, *278**, *281**, *284**, *285*, *287*, *291**, *292*, *295*, *297*, *299* (DUSS; *275* also CTES, M, SP; *275*, *276*, *277*, *278*, *284* also MO). Buenos Aires, *Cleland 1967-508** (CTES, DUSS, MO). TUCUMÁN: Rio Salí near Tucumán, "El Cadillal," *Göpel in 1961** (DUSS, MO). CORRIENTES: Santo Tomé, *Krapovickas 16404* (DUSS, MO).

URUGUAY. COLONIA: Sandy places at roads in western part of Juan L. Lacaze, *Santarius 68***, *72* (DUSS; *68* also M, MO).

BRAZIL. PARANÁ: Corredeira Paulista at Rio Jaguariaiva near São José da Bôa Paulista, *Hatschbach 25564* (DUSS).

CULTIVATED: *O. argentinae* from Erlangen, Germany, received 1960* (CTES, DUSS, M, MO).

Representative specimens examined:

BRAZIL: SÃO PAULO: Alto da Serra, *Gehrt 39948* (POM, SP). PARANÁ: Curitiba, *Dusén 13292* (F, MO, S), *2219* (R), *15827* (GH, LE, NY, S). Jaguariaiva, *Dusén 13189* (S, SI). SANTA CATARINA: Itajai, *Klein 6859* (HBR, RSA). Nova Teutonia, *Plaumann 583* (RB). RIO

GRANDE DO SUL: Uruguaiana, *Vidal 01328* (R). Rio Grande, *Malme 110* (S). Rio Pardo, *Jürgens in 1923* (B). Pôrto Alegre, *Lindmann 363* (S).

URUGUAY. RÍO NEGRO: Near Mercedes, isles of Río Negro, *Rosengurtt 855* (POM). SAN JOSÉ: Río Santa Lucía, *Rosengurtt 859* (POM). FLORIDA: La Palma, *Herter 2105* (F, MO, US, Z).

PARAGUAY. Villarica, *Jörgensen 4117* (C, F, MO, NY, S, SI, US). Villa Elisa near Asunción, *Pedersen 5118* (C). Botanical Garden of Asunción, *Rojas 3174* (POM). Asunción, *Balansa 2219* (K, P, RSA). Sierra de Maracayú near river Capibary, *Hassler 4409* (BM, K, NY, P, UC, W). Sma. Trinidad, *Zürcher in 1913* (Z). Without exact locality, *Bonpland in 1833* (P).

ARGENTINA. BUENOS AIRES: Tigre near Garín, *Lanfranchi 485* (LP). El Socorro near Pergamino, *Parodi 7401* (GH). Campana, *Krapovickas 2593* (BAB, LIL); *Hunziker 1044* (CORD, LIL, RSA). Juinez, *Molfino 146* (POM). Est. Las Palmas near Port. Zárate, *Boelcke 13152* (BAA). Villa Ortuzor, *Parodi 9900* (K, POM, US). Isla Paulino, *Cabrera 7385* (F, GH). Ramalla at Río Paraná, *Burkart 12767* (SI). Pavón at Río Paraná, *Pennington 171* (CORD). Isla Maciel, *Krapovickas 222* (LIL). Federación, *Birabén 5127* (LP). MISIONES: Villa Venecia near Leandro N. Alem, *Krapovickas & Cristóbal 15970* (BAB, CTES, MO). Deseado near Frontera, *Pierotti 5248* (LIL). 20 km S of Bernardo de Irigoyen, 150 m, *Krapovickas & Cristóbal 13714* (BAB, C, CTES, UC). Puerto Polana near Cainguas, *Schwarz 7920* (LIL). Corpus, *Scala* 257 (LIL). Santa Ana, *Rodriguez 647* (GH, LIL, POM, SI, UC). Orera near Candelaria, *Pierotti 5265* (LIL). Loreto near Candelaria, *Montes 14665* (NY). Garupá near Candelaria, *Bertoni 2377* (BM, F, LIL, S). Puerto Cazador near San Ignacio, *Schwartz 4900* (LIL). Posadas, *Grondona & Spegazzini 1111* (BAB). Puerto Istuela near Iguazú, *Montes 9291* (GH, LIL). Eldorado near Iguazú, *Schmidt 2097* (LIL). Apóstoles, *Krapovickas et al. 15485* (CTES). CORRIENTES: Paso de la Patria near San Cosmé, *Tressens et al. 119* (BAA, CTES, F, LP, MO); *Ibarrola 775* (LIL, NY). San Luis de Palmar, *Ibarrola 3260* (LIL). Laguna Rincón near Gral. Paz, *Schwarz 8554* (LIL). Loma Alta near Ituzaingó, *Pierotti 600* (LIL). Between Río Empedrado and Ruta 12, *Quarín & Schinini 1297* (CTES, MO). Est. "Ita Caabó" near Mercedes, *Pedersen 6159* (C, GH, K, US). Est. "Santa Teresa," *Pedersen 117* (P, S, US). Santa Ana, *Parodi 12061* (BAA). Dep. Capital, between Arroyo Riachuelo and Ruta 12, *Krapovickas & Cristóbal 13559* (CTES, MO). Tabay near Concepción, *Krapovickas & Cristóbal 11709* (CTES, K, US). Loreto near San Miguel, *Mroginski 42* (CTES). Laguna Mansa near Paso de los Libres, *Schinini 7603* (CTES, MO). ENTRE RÍOS: Paraná, *Boelcke 1268* (BAA). Isla del Pillo near Victoria, *Burkart 8735* (F, POM). Colón, *Burkart 24874* (MO). Ibicuycito, *Burkart 27309* (MO). San Carlos near Concordia, *Crovetto & Grondona 4139* (BAB). Delta del Paraná, Arroyo Martinez, *Boelcke 901* (BAA). Federación, *Meyer 11131* (LIL). FORMOSA: Colonia Pastoril, *N.N. 98* (BAB). CHACO: Margarita Belén, *Aguilar 1078* (LIL); *Stuckert 19370* (CORD). Las Palmas, *Jörgensen 2489* pro parte (POM). Fontana, *Meyer 455* (LIL, POM, SI). Vis-a-vis of Corrientes, *Alboff in 1890* (NY). Colonia Benítez, *Schulz 502* (POM), *10075* (BAB). SANTA FÉ: Mocoví, *Venturi 94* (BAB, CORD, LIL, P, POM, SI). Guadalupe, *Huidobro 3389* (LIL, RSA). Esperanza near Las Colonias, *Huidobro 3263* (LIL, RSA). Colonia Mascias near Garay, *Pueyo 105* (CTES). Rosario, *Burkart 8772* (F, SI). Laguna Setubal, *Alvarez 807* (LIL). San José del Rincón, *Alvarez in 1916* (LIL). San Justo, *Erbaggi & León 966* (SI). San Cristóbal, *Balegno 593* (LIL). Reconquista, *Parodi 11129* (POM), *11146* (BAA, POM); *Burkart 5795* (F, SI). SANTIAGO DEL ESTERO: Colonia Jaimez near Robles, *Luna 1329* (LIL); *Ruiz in 1948* (RSA). Zurena near Robles, *Maldonado 441* (LP). La Isleta between Ceres and Colonia near Rivadavia, *Hunziker 10384* (CORD). Selva near Rivadavia, *Balegno 462* (LIL). Parque Aguirre in Santiago del Estero, *Argañaraz 440* (LIL). El Puestilo near Guasayán, *Cuezzo 2405* (LIL). La Banda, *O'Donell 4248* (LIL). CÓRDOBA: *Hieronymus in 1878* (BR, FR, K, LE, P). San Vicente, *Kurtz 576, 577* (CORD). Río Primero, *Kurtz 2625* (CORD). Capilla del Monte, *Hossens 364* (CORD). Emp. Tanti near Punilla, *De la Sota 3075* (LIL). Río Segundo, *Sublis 1080* (CORD). Ascasubi near Tercero Arriba, *Krapovickas 6391* (BAB, CORD). Cárcano near San Martín, *Krapovickas 7403* (LIL). Casa Bamba near Colón, *Stuckert 23732* (CORD). Near Villa Dolores, *Hunziker 13204* (RSA). Alta Gracia, *Hunziker 6761* (CORD, LIL). Est. La Redución in the Sierra Chica, *Pastore 348* (SI). SAN LUIS: *Burkart 12086* (SI). JUJUY: Agua Negra near Ledesma, *Fabris et al. 3044* (LP). Villa Achaval, *Cabrera 20059* (LP). SALTA: Río San Francisco near Orán, *Rodríguez 1155* (GH, LIL, POM, SI). Puerta Verde near Santa 2° sección, *N.N. 603* (LIL-216719). Vallecito near Metán, *Lenna 384* (LIL). TUCUMÁN: Cerro San Javier, *Boelcke 2911* (BAA, MO). Río Salí, *Venturi 898* (BAA, GH, LIL, POM, SI, US). Chañar Pogo near Leales, *Venturi 491* (LIL, LP, MO, POM, SI). Agua Dulce near

Leales, *Monetti 1163* (GH, LIL). Río Colorado near Famaillá, *Carenzo 3425, 2429* (LIL). Yerba Buena, *Meyer in 1949* (LIL). El Morado near Burroyacú, *Peirano 10085* (LIL). CATAMARCA: Andalgala, *Jörgensen 1054* pro parte (LIL). Choya near Andalgala, *Castillon 14417* (GH, LIL). San Antonio, *Castillon 1283* (LIL). Río del Valle near Piedra blanca, *Lillo 9085* (LIL). LA RIOJA: Quebrada de Soria, 8 km SE of Chamical, *Hunziker 16638* (CORD). Nonogasta, *Castellanos 27-2011* (POM). F. Belgrano, *Gomez 66* (LIL). Dique de Alta, *Hunziker & Fabris 14441* (CORD). SAN JUAN: Valle Fertil, *Hunziker 16698* (CORD).

Specimens from outside of South America (naturalized):

GERMANY. Humboldt mill near Tegel, Berlin, *Schulz in 1896* (B). Port of Ludwigshafen, *Zimmermann in 1907* (L). Port of Neuss, *Bonte in 1926* (BAS). Finkenwerder near Hamburg, *Christiansen in 1926* (BAS). Emmerich, 1930, *Kern & Reichgelt 12180* (L).

NETHERLANDS. Wormerveer, 1913, *Kloos 57* (L), *in 1916* (L), *in 1923* (L). Rotterdam, 1904, *Jansen & Wachter 13287* (L), *in 1920* (L); *Kloos in 1920* (BAS, L).

FRANCE. Dép. Nord, Dunkerque, 1926, *Bouly de Lesdain 585* (BAS).

PORTUGAL. Barreiro near Estremadura, 1958, *Rainha 3703* (LISE). Moita, 1961, *Rainha 4844* (LISE).

RHODESIA. Distr. Selukwe, Ferny Creek, ca. 1,190 m, 1953, *Wild 4281* (K, MO, SRGH); 1966, *Biegel 1498* (SRGH). Distr. Gwelo, 1,280 m, 1965, *Biegel 475* (SRGH).

BOTSWANA, Distr. South Eastern, Gaberone, Content Farm, 1972, *Kelaole A 78* (SRGH).

SOUTH AFRICA. TRANSVAAL: Near Pretoria, 1930, *Moss 18261* (BM). Distr. Letaba, 1958, *Scheepers 270* (BM, K, MO, PRE, SRGH). Duiwelskloof, 945 m, 1958, *Scheepers 270* (K). Distr. Wolmaranstad, *in 1963* (PRE-29488). Pta. Harde near Eloffsdal, 1963, *Hanekom 1663* (K, SRGH). NATAL: Distr. Ifafa River, ca. 610 m, 1948, *Gerstner 6932* (PRE). Distr. Port Shepstone, St. Michaels-on-Sea, 1966, *Strey 7094* (K). Distr. Umzinto, Shelley beach, 1967, *Strey 7284* (K). ORANJE FREE STATE: Bloemfontein, 1956, *Gemmell 6737* (K). Distr. Swinburne, Rensburgshop, 1961, *Jacobsz 91* (PRE). Distr. Kimberley, ca. 1,220 m, 1961, *Leistner 2931* (K, PRE). Distr. Frankfort, *Strydow* (K, PRE). LESOTHO: Maseru, 1969, *Williamson 22* (K, SRGH). CAPE: Hout Bay near Rondebosch, 1932, *Adamson 2198* (BM). Cape Peninsula, 1933, *Salter 4001* (K). Kuils River, near Bellville, 1953, *Parker 4849* (K). Stellenbosch, 1952, *Parker 4839* (K); 1964, *Taylor 5643* (K).

SOUTH WEST AFRICA: Windhoek mountains, Grundschwel near Finkenstein, 2,000 m, 1965, *Seydel 4223* (MO).

TRISTAN DA CUNHA: *Stableford in 1953-54* (K).

AUSTRALIA. NEW SOUTH WALES: Birdwood near Yarras, *Noonen in 1961* (NSW-135161). "Carp View" near Gilgandra, *Holawich in 1965* (NSW-135156). La Peraouse, *Coveny in 1965* (NSW), *in 1966* (NSW-135166). Morpeth, 1972, *Johnson 7538* (NSW).

Oenothera indecora subsp. *bonariensis* reported in literature from outside of South America:

SOUTH AFRICA: Jacot-Guillarmod (1971); Ross (1972: 262).

GERMANY: Léveillé & Thellung (1918).

FRANCE: Fournier (1937: 598, as *O. argentinae*).

Hybrids between *O. indecora* subsp. *bonariensis* and *O. stricta* subsp. *stricta* occur in Australia and Portugal.

AUSTRALIA. NEW SOUTH WALES: Warialda, *Lanagan in 1950* (NSW-135159). Casino Distr., *Glenfield in 1950* (NSW-135162). Narraben, *Mair in 1953* (NSW-68289). Patagona Beach, *Coans in 1954* (NSW-66109). Grafton, *Flynn in 1954* (NSW-66107). Warialda, *Grullan in 1956* (NSW-135158). Grafton, *O'Grady in 1957* (NSW, RSA). Moree Distr., *Mactier in 1962* (NSW-135155). Premer, *N.N. in 1962* (NSW-135157). Ashford, *McNamara in 1963* (NSW-135160). Menangle Park, 1964, *McBarron 9507* (NSW). Sackville Reach near Hawkesbury River, *Walker in 1965* (NSW-135164). Dee Why Laggon, *Coveny in 1966* (NSW-126453). Narrabeen Lake, *Coveny in 1966* (NSW-135165). Near Iluka, ENE of Maclean, 1969, *Coveny 2178* (NSW, DUSS).

PORTUGAL. ESTREMADURA: Moita, 1954, *Rainha 2703* (COI, LISE), 1961, *Rainha 4847* (LISE); Caldas da Rainho, 1960, *Rainha 4425* (COI, LISE); Costa da Caparics, *Matos in 1967* (COI).

Despite its extensive range, *O. indecora* subsp. *bonariensis* is very uniform, in contrast, for example, to *O. odorata* with its seemingly endless variability. This might be related to the great ecological amplitude of *O. odorata* and the

FIGURE 166. *Oenothera punae* (Bolivia, La Paz, *Santarius 2013*); *Oenothera* sect. *Oenothera* subsect. *Munzia*.

much more limited range of habitats in *O. indecora* subsp. *bonariensis*, which flourishes only in sandy places.

At least a major portion of the chromosomal complex of *O. indecora* subsp. *bonariensis* is represented in the chromosomally heterozygous entities *O. picensis* subsp. *bonariensis* and *O. parodiana* of series *Allochroa*, as well as in *O. brevipetala*, *O. tucumanensis*, and *O. punae* of series *Clelandia*.

The chromosomal heterozygotes from Uruguay (*Santarius 68, 72*) have two complexes derived within *O. indecora*. The relatively short bracts of these plants suggest, however, that one of these complexes may be modified by genes from *O. ravenii*, probably transmitted to *O. indecora via* the small-flowered *O. parodiana*.

19c. **Oenothera indecora** subsp. **boliviensis** Dietrich, subsp. nov.

Plantae maxime ad 20 cm altas, bene ramosae. Pubes ut in subsp. *bonariensis*. Folia caulina 2–3 cm longa, 2–3 mm lata; bractea 1.5–2 cm longa, 1.5–2 mm lata. Gemmae 2–3 mm longae, 1.5–2 mm crassae. Petala 2–3 mm longa. Capsula 1.5–2 cm longa. Semina ambito elliptica, 0.8–1 mm longa, 0.3–0.4 mm crassa. Cleistogama. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice homozygotica.

Plants attaining a height of only 20 cm, bushy and well branched. Pubescence as in subsp. *bonariensis*. Cauline leaves 2–3 cm long, 2–3 mm wide; bracts 1.5–2 cm long, 1.5–2 mm wide. Buds 2–3 mm long, 1.5–2 mm thick. Petals 2–3 mm long. Anthers 1.5–2 mm long. Filaments 1.5–2.5 mm long. Capsule 1.5–2

cm long. Seeds elliptic in outline, 0.8–1 mm long, 0.3–0.4 mm thick. Cleistogamous. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I).

Type: Cultivated in the Botanical Garden of Düsseldorf, Germany, 8 Aug. 1972. Source: Bolivia, near La Paz, *A. Hecht 1964-29* (MO-2155715, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 233): Known only from the type locality.

Specimen examined from cultivated plants:
BOLIVIA. LA PAZ: La Paz, *Hecht 1964-29** (CTES, DUSS, M, MO).

This subspecies seems clearly to be a derivative of subsp. *bonariensis* and is thus far known only from cultivation. It might very possibly be a chromosomally homozygous derivative of the complex heterozygote *O. punae*, which in turn has been derived by the combination of various species of series *Renneria* with *O. indecora* subsp. *bonariensis*. The range of subsp. *bonariensis* extends to high enough elevations in the province of Salta so that this combination is possible. If this reasoning is correct, then *O. indecora* subsp. *boliviensis* provides an excellent demonstration of the way in which a genome can be altered when it is combined in a complex heterozygote. The F_1 generation derived by hybridizing *O. indecora* subsp. *bonariensis* with *O. punae* segregated, as might be expected, into two distinct classes of plants, one of which has the habit of *O. punae*, the other the more normal habit of *O. indecora*. This indicates that the normal habit of subsp. *bonariensis* is dominant over the nanism of subsp. *boliviensis*.

The absence of *O. indecora* subsp. *boliviensis* as a wild plant might be explained on the hypothesis that its genome can exist at high elevations only in combination with those derived from series *Renneria*. It should however be sought in the vicinity of La Paz, Bolivia.

20. **Oenothera affinis** Cambess. in St.-Hilaire, Fl. Bras. Mer. 2: 269. 1829.—FIGS. 58–59, 133, 180–181, 218.

O. berteriana Spach, Nouv. Ann. Mus. Hist. Nat. 4: 343. 1835. TYPE: Chile, Prov. Valparaíso, Quillota, *Bertero* (P, holotype, F and GH photographs; G, isotype); Ann. Sci. Nat. Bot., sér. 2, 4: 273. 1835.

O. chilensis Fischer & Meyer, Ind. Sem. Hort. Bot. Petrop. 45. 1835. LECTOTYPE: Cultivated in the Botanical Garden at Leningrad from seeds of the Botanical Garden at Paris, 1835 (LE).

O. macrosiphon Lehm. ex Otto, Hamburger Garten- Blumenzeitung 14: 439. 1858. Based on plants cultivated at Hamburg, the seeds received from Darmstadt as *O. villosa*; authentic material not seen. A contemporary specimen bearing this name, probably cultivated in Berlin, was in the K. Koch herbarium in Berlin until it was destroyed in World War II; a photograph and fragments are at POM.

O. mollissima L. var. *grandiflora* Micheli in Mart., Fl. Bras. 13(2): 178, *tab.* 38. 1875, pro parte.

Onothera polymorpha H. Lév. race *propinqua* (Spach) H. Lév. var. *berteriana* (Spach) H. Lév., Monogr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 324. 1909.

Raimannia berteriana (Spach) Sprague & Riley, Bull. Misc. Infor. 1921: 200. 1921.

Oenothera diplotricha Domin, Bibl. Bot. 22(89): 992. 1928. TYPE: Australia, South-Queensland, mixed forests at Logan River, on sand, 1910, *K. Domin III*. Not located.

O. mollissima sensu Munz, Physis 11: 282. 1933, pro parte; Amer. J. Bot. 22: 659. 1935, pro parte; Revista Univ. Chile 22. 1: 266. 1937, pro parte; Comun. Bot. Mus. Hist. Nat. Montevideo 1(10): 29. 1943, pro parte.

FIGURE 167. *Oenothera laciniata* subsp. *pubescens* (Peru, Junín, *Santarius 2190*).

O. mollissima "El Cuadrado" Cleland, Jap. J. Genet. 43: 332. 1968.
Oenothera affinis "longiflora Erlangen" Cleland, Jap. J. Genet. 43: 332. 1968.

Erect annual herb, not forming a rosette, unbranched or ± well branched throughout, 4–15 dm tall. Entire plant covered with soft hairs, densely to sparsely long-villous, the hairs erect, densely short-villous, and densely glandu-

lar-pubescent. Cauline leaves cultrate to narrowly lanceolate, acute, acute to rounded at the base, sessile, 5–15 cm long, 0.5–1.5 cm wide; bracts cultrate to narrowly lanceolate, acute, rounded to truncate at the base, sessile, longer than the capsules they subtend, (3–)4–9 cm long, 0.5–1.2 cm wide; leaves plane or weakly to evidently undulate at the margins, sparsely serrate with blunt teeth. Inflorescence branched. Floral tube 8–11(–13) cm long. Buds narrowly lanceolate to lanceolate in outline, green or yellowish green, often flushed with red, 2–3.5 cm long, 6–9 mm thick; apices of the sepals erect or divergent, 1.5–4 mm long. Petals very broadly obovate, (1.5–)2–4 cm long. Anthers 10–14 mm long. Filaments 15–20 mm long. Style long or short, the stigma held above the anthers at anthesis or surrounded by them, 9–13.5 cm long. Stigma lobes 5–10 mm long. Ovary 1.3–2 cm long. Capsule (2–)2.5–4(–5) cm long, 3–4 mm thick, thicker in the upper third, and with the 4 valves clearly separated at the apex. Seeds elliptic in outline, 1.5–2 mm long, 0.5–0.6 mm thick. Self-compatible; outcrossing or self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 14** or intermediate configurations at meiotic metaphase I). Flowering time: Brazil, Uruguay and eastern Argentina, September–May; central Argentina, October–April; Bolivia, Chile and northern Argentina, November–April.

Type: Brazil, Rio Grande do Sul, margins of woods near city of Rio Pardo, April (1816–1821), *Auguste de St.-Hilaire 2791-12* (P, holotype, F and GH photographs).

Distribution (Figs. 234, 244): In Brazil from Rio de Janeiro through Minas Geraís to Rio Grande do Sul. Apparently absent in the Atlantic departments of Uruguay, but frequent in the western, central, and southern departments of Ártigas, Salto, Paysandu, Río Negro, Soriano, Colonia, Flores, San José, Tacuarembo, Durazno, Florida, Canelones, and Montevideo. From northern Argentina the species extends to Tarija in Bolivia. It occurs throughout northern Argentina, where it ascends to an elevation of 2,500 m along the river valleys of the Andes, and in central and eastern Argentina. It occurs in the following provinces of Argentina: Jujuy, Salta, Tucumán, Catamarca, La Rioja, San Juan, Mendoza, Chaco, Formosa, Santiago del Estero, Santa Fé, Córdoba, San Luis, La Pampa, Misiones, Corrientes, Entre Ríos, and Buenos Aires. West of the Andes, the species occurs in Chile from the province of Atacama to Valparaíso.

Specimens examined from cultivated plants:

URUGUAY. MONTEVIDEO: Garden of the Facultad de Agronómia in Montevideo, *Santarius 193** (ring 6, 4 bivalents), *194-196*, *197**, *198-204* (DUSS; *193*, *197* also CTES, M, MO). Toledo, *Hecht 1964-95*** (CTES, DUSS, M, MO). Botanical Garden of the Facultad de Agronómia in Montevideo, *Rosengurtt B11256* (ring 6, 4 bivalents) (DUSS). FLORIDA: At the railroad about 1 km NE and 3 km SW of Mansavillagra, *Santarius 215*, *217*, *218* (ring 12, 1 bivalent), *220*, *222** (ring of 8, 3 bivalents), *223*, *224*, *225**, *226*, *228**, *229*, *230* (DUSS; *218*, *222*, *225*, *228* also CTES, M, MO). 3 km S of Arrayán at Ruta 7 near the Río Mansavillagra, *Santarius 242*** (DUSS). Florida, *Hecht 1964-1*** (DUSS, M, MO).

ARGENTINA. BUENOS AIRES: Garden of the Botanical Institution of the Facultad de Agronómia in Buenos Aires, *Santarius 259*, *261* (DUSS). Old gravel mine E of the road from Berisso to Los Talas, about 1 km SE of Villa Zula near La Plata, *Santarius 300**, *301**, *302*, *304*, *308-312*, *314**, *315-317*, *319*, *321*, *324-326*, *328* (DUSS; *300* also CTES, M; *300*, *310* also MO). Punta Lara near La Plata, *Gopel in 1961* (DUSS); *Hecht 1964-97* (DUSS). Botanical Garden of Buenos Aires, *Diers 19** (DUSS, M). Villa Ortuzor in Buenos Aires, *Hecht 1964-125** (CTES, DUSS, M, MO). ENTRE RÍOS: Gualeguaychi, Parque Unzue, *Burkart 23060*

(DUSS). Isla Almiron Chico near Concepción del Uruguay, *Burkart 23062* (DUSS). SANTA FÉ: Santa Fé, *Cleland 1965-426** (DUSS). CÓRDOBA: Córdoba, *Hecht 1964-90* (DUSS). El Cuadrado, *Cleland 1967-417*** (DUSS). SALTA: Dep. Cafayate, Tolombón near the border of Tucumán, 1,600 m, *Hunziker 21104* (CTES, DUSS, MO). JUJUY: In the bed of Río Xibi S of San Salvador de Jujuy, 1,250 m, *Santarius 1841***, *1842*, *1843* (DUSS; *1841* also MO). In the bed of Río Grande N of San Salvador de Jujuy, 1,250 m, *Santarius 1849***, *1850** (DUSS; *1850* also CTES, M, MO). Road to Pucara, 1 km S of Tilcara, 2,450 m, *Santarius 1851**, *1852** (DUSS; *1851* also CTES, M, MO). Damp slope NE of Tilcara, about 150 m N of the cemetery, 2,500 m, *Santarius 1853**, *1854*, *1855*, *1857*, *1860*, *1863*, *1867*, *1869**, *1870-1872*, *1877*, *1878*, *1881*, *1882*, *1884* (DUSS; *1869* also CTES, M; *1869*, *1882* also MO). TUCUMÁN: Stony places, Río Salí, near the bridge of Ruta 9, E of San Miguel de Tucumán, 420 m, *Santarius 1672***, *1674*, *1675** (DUSS; *1672*, *1675* also M, MO). Bed of Río Lules, N and NW of Lules, 410 m, *Santarius 1679**, *1680* (ring of 6, ring of 4, 2 bivalents), *1682*, *1685*, *1687*, *1693*, *1695*, *1697*, *1699*, *1702*, *1709*, *1711** (ring of 4, 5 bivalents) (DUSS; *1711* also CTES, M; *1680*, *1697*, *1711* also MO). Bed of Río Seco near bridge at Ruta 38, 450 m, *Santarius 1712* (ring of 8, 3 bivalents) (DUSS). Bed of Río Gastona near the bridge at Ruta 38, 450 m, *Santarius 1713* (ring of 6, 4 bivalents (DUSS, MO). Bed of Río Angostura, from Tafí del Valle to 5 km N, 2,000–2,250 m, *Santarius 1714**, *1718*, *1722*, *1724*, *1727*, *1730* (DUSS; *1714* also CTES, M; *1714*, *1727* also MO). Bed of Río Angostura at km 24.5 of Ruta 307 near Tafí del Valle, 800 m, *Santarius 1788** (ring of 8, 3 bivalents), *1789–1791*, *1794*, *1799*, *1800* (DUSS; *1788*, *1799* also MO). At km 16.5–17, 570 m, *Santarius 1801* (ring of 8, 3 bivalents; ring of 8, ring of 4, 1 bivalent) (DUSS, MO). At km 11 in the bed of Río Totorilla, 430 m, *Santarius 1802* (ring of 4, 5 bivalents), *1803*, *1804* (DUSS; *1802* also MO). Clavillo near Tucumán, *Cleland 1967-425** (CTES, DUSS, M, MO). LA RIOJA: Costadero to Mina, *Hecht 1964-120** (CTES, DUSS, M, MO, SP).

CHILE. COQUIMBO: Dry place at a road in a vineyard near Pisco del Elqui, *Stubbe in 1961* (ring of 12, 1 bivalent).

CULTIVATED. *O.* "*longiflora*" from the Botanical Garden in Erlangen, Germany, received 1962* (CTES, DUSS, M, MO).

Representative specimens examined:

BRAZIL. MINAS GERAÍS: Caldas, *Hoehne 2799* (POM, SP). Between Carandaí and Crespo, *Duarte 524* (BR). Morro de Cruzeiro near Ouro Preto, *Emygdis 2881* (R). RIO DE JANEIRO: Villa Theresa, *Glaziou 8344* (G, K, LY, P). SÃO PAULO: Pinheiros, *Usteri 11896* (SP). São Paulo, *Hoehne 11670* (POM). Ipanema, *Galvão in 1884* (R). Belémsinho, *Porto 11670* (SP). PARANÁ: Oure Fine near Bocayúva do Sul, *Hatschbach 963* (HB). Rio Jangada near Palmas, *Hatschbach 3493* (RSA). Serro Azul, *Rambo 11199* (SP). Rio Cavernoso near Guarapuava, *Pereira 7696* (HB). Rio Perdido near Laranjeiras do Sul, *Hatschbach 19855* (UC). SANTA CATARINA: Garopaba, *Klein & Bresolin 8850* (HBR). Valley of Rio Pelotas, *Pabst & Pereira 6224* (HB). Lajes, Morro do Pinheiro Seco, 1,000 m, *Reitz 6601* (HBR). Itapiranga, 200 m, *Klein 5200* (HBR, RSA). Banks of Rio Uruguai near Mondaí, *Smith & Reitz 9728* (HBR, R, RSA, US). Ubatuba, *Hans 311* (R). RIO GRANDE DO SUL: Banks of Rio Ibira Puitan near Alegrete, *Palacios & Cuezzo 1837* (LIL). Rio Pardo, *Jörgens 16* (B). Serro Largo, *Sehnem 3549* (SI). Between S. Angelo and Guarani das Missões, *Santos 2727* (R).

URUGUAY. ÁRTIGAS: Arroyo Tres Cruces Grande, *Praderi 2540* (LIL). SALTO: San Antonio, *Osten 5423* (SI). PAYSANDÚ: M. Cassioni, *Puerto 8303* (MVFA). SORIANO: Fray Bentos, *Fruchard in 1877* (P, RSA, US). Sta. Elena, *Rosengurtt PE-4386* (GH, LIL, MO, SP). COLONIA: Colonia Valdense, *Dubugnon 77* (G). TACUAREMBO: Valle Edén, *Arrillaga 1733* (MVFA). DURAZNO: Between Río Negro and Est. km 329, *Ziliani 10549* (MVFA). FLORIDA: Mansavillagra, *Rosengurtt B791* (GH, POM). FLORES: Río Yi, *Rosengurtt B564* (POM). SAN JOSÉ: Barra Santa Lucia, *Osten 4551* (G). Arazati, *Rosengurtt 1696* (POM). CANELONES: Arroyo de Saúce, *Bartlett 20963* (GH, MICH, NY, P, UC, US). MONTEVIDEO: Sta. Lucía, *Fruchard in 1972* (P). Colón, *Osten 3714* (G). Montevideo, *Isabelle in 1838* (W).

PARAGUAY. Alto Paraná, *Montes 9929* (LIL).

BOLIVIA. TARIJA: Tarija, *Fries 1125* (S); *Zelada 41* (LIL); 2,000 m, *Fiebrig 2435* (BM, G, K). Padcaya, 2,100 m, *Fiebrig 2545* (BM, G, LY).

ARGENTINA. JUJUY: Yala, 1,600 m, *Arnow 3747* (MO). Tilcara, ca. 2,400 m, *Balls 5955b* (F, K, UC, US); *Meyer in 1940* (F, GH, LIL-33737, NY, SI). Quebrada de la Huerta near Huacalera, 2,700 m, *Cabrera 12041* (BAB). El Fuerte near Sta. Báebara, *Cabrera 17273* (BAA, LP). SALTA: La Candelaria, 1,200 m, *Schreiter 9436* (GH, LIL). Pampa Grande, *Hohnberg 6906* (BAB). El Morenillo near Rosario de la Frontera, 690 m, *Carbone 10088* (LIL). Victoria, *Meyer 5040* (LIL, UC). Cachí, *Garolera-Romero in 1947* (LIL, RSA).

Tolombón near Cafayate, 1,600 m, *Hunziker 21104* (CORD, MO); *Hayward 002066* (LIL). TUCUMÁN: Río Churqui, *Lillo 7512* (LIL, US). Río Salí near Tucumán, 600 m, *Venturi 999* (GH, LIL, POM, SI, US). Río Cochuna near Chicligasta, 915 m, *Munz 15476* (GH, NY, POM, US). Tafí del Valle, *Araque & Barkley 19Ar161* (F, LIL). Cerro Muñoz near Tafí, 2,500 m, *Lillo 1241* (LIL). Río Lules, 760 m, *Mexia 04354* (GH, MO, UC). Río Tipamayo near Trancas, *Venturi 4218* (GH, LIL, NY, POM, US). S. Pedro de Colalao near Trancas, *Krapovickas & Cristóbal 15339* (CTES). Cerro del Campo near Burroyacú, 2,000 m, *Venturi 7748* (K). CATAMARCA: Andalgala, *Jörgensen 1054* (BAB), *1055* (GH, LIL, MO, POM, SI); *Rodríguez 344* (GH, LIL, S, UC). Río Pomancillo, *Spegazzini 29563* (BAB). San Antonio near Padín, *de Ance in 1957* (SI). El Portezuelo, *Bartlett 19613* (MICH, US). Yacutula near Belén, *Schickendandz 131* (CORD, GOET). Barranca Larga near Belén, 2,400 m, *Schreiter 10248* (LIL). Near Capayán, *Risso 556, 565, 626, 770* (LIL). Sta. María, Cerillos, 3,000 m, *Peirano in 1933* (LIL). Sierra de Ambato, between Mutquin and Pomán near Colana, 1,650 m, *Hunziker et al. 18406* (CORD, MO). LA RIOJA: Sierra Famatima, Alto Carrizal, *Calderon 1044* (BAA). La Hoyada, 2,500 m, *Kurtz 15041* (CORD, MO). Guanchin Viejo, *Castellanos 28-284* (BA, POM). Santa Cruz, *Toscani 32* (BAB). Campanas, 1,850 m, *Rojas Paz in 1942* (GH, LIL, NY). Rodeo de Las Vacas, 3,000–4,000 m, *Flossdorf 40* (SI). Dep. Capital, El Cantadero, 1,200 m, *Meyer 3939* (GH, LIL, UC). Sierra de Velazco, El Cantadero, 2,300 m, *Hunziker 5270* (CORD, SI). Yacuchi, *Kurtz 15414* (MO). Punta de Agua near Gral. Sarmiento, 2,600 m, *Hunziker 2083* (CORD, POM). Los Molles near Lamadrid, 2,700 m, *Krapovickas & Hunziker 5530* (BAB, CORD). SAN JUAN: Between Rodeo and Colanguil near Iglesias, *Castellanos 15495* (US). Dep. Calingasta, Las Lumbreras, 2,000 m, *Spegazzini 656* (BAB). Río Calingasta near Calingasta, *Zarchini 150* (CTES). Quebrada de Huachi near Jachal, 1,500 m, *Rodrigo 2993* (LP). Chimbas near Desamparados, *Cuezzo 1266* (LIL, RSA). Valle Fertil, *Hunziker 16686* (CORD). Villa Krause near Pocitos, *Cuezzo 2175* (LIL). La Bebida near Rivadavia, *Cuezzo 1433* (LIL). MENDOZA: *Philippi 614a* (SGO). Junín, *Ruiz Leal 7033* (Leal, LIL). FORMOSA: *Hicken* (SI-4851). Pirané, *Morel 638* (LIL). Uriburú at Río Bermejo, *Kermes 68660* (BAB). CHACO: Las Palmas, *Jörgensen 2488* (GH, LIL, SI, US). Resistencia, *Meyer 3212* (LIL, POM). Fontana near Resistencia, *Meyer 456* (LIL, SI). Colonia Benítez, *Stuckert 19511* (CORD, G); *Schulz 501* (POM). Fortín Anguilar, *Hossens in 1917* (CORD). SANTIAGO DEL ESTERO: Dep. Rivadavia, between Selva and Palo Negro at Ruta 34, 100 m, *Hunziker 17776* (CORD, MO). SANTA FE: Mocoví, *Venturi 275* (SI); *Quarin 1145* (CTES). Monje, *Pedelaborde in 1940* (LIL, SI). At Ruta 9 across the Río Caracaraná near Iriondo, *Hunziker 13702* (CORD, MO). Reconquista, *Venturi 275* (LIL, POM). Las Colonias near Pilar, *Terribile 474* (LIL). Aurelia near Castellanos, *Terribile 490* (LIL). CÓRDOBA: Banks of Río Primero near Ojo de Agua, *Hunziker 11920* (CORD, MO). Gral. Paz, *Stuckert 3730* (CORD, G, MO). Sierra San Ignacio near Quintas, *Stuckert 18586* (CORD, G). Dique Los Molinos near Calamuchita, *Krapovickas & Cristóbal 14714* (CTES). Río Tercero, *Burkart 10369* (MO, SI). Near Santa María, *Krapovickas 6514* (BAB, CORD, LIL). Capilla del Monte, *Nicora in 1941* (SI-17600). Totoral, *Domínguez 106* (POM). La Carlota near Juárez Celman, *Hossens 385* (CORD). Córdoba, *Lorentz 308* (CORD, GOET); *Hieronymus in 1878* (FR); *Lossen 128* (G, LE, M, SI, Z). Ascochinga, *Giardelli 845* (SI). Las Compuertas at Río Segundo, *Sublis 1171* (CORD, MO). Sierra Chica, between Pan de Azúcar and Villa Allende, *Hunziker 11932* (RSA). Cruz del Eje, *Meyer 13042* (LIL). San Javier, *Castellanos 10734* (RSA); *Fabris & Moreau 6791* (BAB, LP). Capilla del Monte, *Hossens 427* (CORD). Copina, *Hieronymus 333* (P). Los Cocos near Punilla, *De la Sota 3278* (LIL). SAN LUIS: Sierra de Comechingones, El Rincón, *Hunziker 11852* (CORD, MO). Piedra Blanca near Merlo, 1,000 m, *Digilio-Grassi 2066* (LIL, RSA). Trapiche, *Gez 31-278* (POM). Quebrada de los Bueyes, *Galander in 1882* (CORD). LA PAMPA: Between Chamaico and Casimiro Gomez near Rancul, *Cabrera & Sagastegui 19406* (LP). MISIONES: Corpus near San Ignacio, *Schwarz 3411* (LIL, S). Gob. Roca near San Ignacio, *Schwarz 6413* (LIL). San Ignacio, *Quiroga in 1913* (POM). San Pedro, *Bertoni 2101* (LIL). Victoria at Ruta 12 near Iguazú, 170 m, *Schmidt 2743* (LIL). Bonpland near Posadas, *Lilliesköld* (F, S). Garupá near Cainguas, *Bertoni 4660* (LIL). Santa Ana, *Rodríguez 109* (GH, LIL, SI, UC). Candelaria, Ruta 105, *Mroginski 430* (CTES, MO). CORRIENTES: Mercedes, *Rodrigo 711* (LP, NY). Est. "La Pastoril," at Río Paraná near Lavalle, *Pedersen 3858* (BR, C, G, UC, US). Monte Caseros, *Nicora 5748* (BAA, CTES). Paso de los Libres, *Ibarrola 2002* (LIL, NY, S); *Schinini 7698* (CTES, MO). Santo Tomé, *Ibarrola 1233* (LIL, NY). Curuzú Cuatiá, *Spegazzini 154* (BAB). Bella Vista, *Schinini 6565* (CTES, MO). ENTRE RÍOS: Concepción del Uruguay, *Lorentz 628* (BREM, COI, CORD, F, FR, G, HBG, K, L, LE, LY, M, UPS, W, Z), *12* (GOET). Arroyo

Martínez, *Boelcke 907* (BAA). Paraná, *Frommel & Lefebre in 1888* (P). Paracao near Paraná, *Burkart 23762* (MO). Calera Barquin near Colón, *Pozzi 27-1572* (POM). La Paz, *Burkart 21312* (SI). Federación, *Meyer 11130* (LIL). Diamante, *Burkart 22243* (MO, RSA). Isla Almiron Chico, *Burkart 23062* (MO). Gualeguaychú, *Burkart 23060* (MO). BUENOS AIRES: Delta, Río Carabelas near Tiburón, *Scala in 1925* (NY). Est. Las Palmas near Zárate at Río Paraná, *Boelcke 13166* (BAA, MO). Hudson near La Plata, *Eyerdam & Beedle 23156* (G, GH, K, MO, UC). Pereyra near La Plata, *Cabrera 7607* (LP). Palermo, *Munz 15460* (NY, POM, US). Los Talas near Berisso, *Boffa 171* (F, LIL, S). Atucha near Gral. Uriburu, *Krapovickas 3290* (BAB, LIL). *San Isidro, Parodi 8565* (GH). Martín Garcia, *Boelcke 5034* (SI). Otamendi, *Fabris 4995* (LP). Pergamino, *Boelcke 2215* (BAA). Punta Lara, *Dawson 854* (F, GH, LP, NY); *Rodríguez 520* (S, SI).

CHILE. ATACAMBA: Valley of Río Transito, La Pampa near Vallenar, *Johnston 5860* (GH, K, POM). Higuerita near San Félix, 1,300 m, *Ricardi 3867* (CONC). COQUIMBO: *Gay in 1838* (P). Rivadavia, 800 m, *Werdermann 175* (BM, F, G, GH, HBG, LIL, MO, SI, UC, Z). Rapelcillo near Ovalle, 800 m, *Jiles 1958* (CONC). Between Pauhuano and Elqui, *Pfister 6498* (CONC). Tunga near Illapel, *Landbeck in 1962* (SGO). ACONCAGUA: Los Andes, 1,100 m, *Behn 22802* (CONC); *Scott Elliot 436* (BM); *Philippi in 1885* (HBG, SGO). San Felipe, *Claude-Joseph 2508* (US). Chupaja, *Jelinek* (W). Near Papudo, *Zöllner 5168* (L). VALPARAÍSO: *Petre in 1818* (S), *in 1827* (W). Laguna Verde, 100–150 m, *Eyerdam et al. 10040* (F, NY, UC, US). Concón, *Poeppig 121* (BM). Limache, *A.J.H. in 1927* (M). Quillota, *Maximowitsch 133* (LE). SANTIAGO: *Philippi 886* (P, LE). Salto de Conchalí, *Philippi 614b* (SGO); *Marques in 1878* (HBG). Cordillera de Santiago, *Germain in 1856–57* (FR, G, K, W). Cerro de Renca, *Gusinde 643* (W). ISLA JUÁN FERNANDEZ: Cumberland bay, valley of Lord Anson, *Bock in 1931* (SGO). Province unknown: Aeuleo, *Bertero 464, 1185* pro parte (BM, W). Farillar, *Volckmann 28* (SGO).

Specimens from outside of South America (naturalized):

SCOTLAND. Selkirk, 1965, *Webster 10169* (BM, E).

SPAIN. Railway station of San Sebastian, *Guillon in 1877* (MPU). Oña, *Arraiano in 1881* (COI).

PORTUGAL. ESTREMADURA: Sandy places near Lagoa Obidos, *Daveau in 1882* (BM, COI, LISU). Samouco, 1882, *Coutinho 1273* (LISU). Barreiro, *da Cunha in 1888* (LISE, LISU). Trafaria, *Daveau 3093* (BM, LISU); *Jonge in 1912* (BAS). Moita, *da Cunha in 1889, in 1891* (LISE), *in 1890* (LISU). Brejo do Cobre, *Santoz in 1905* (LISU). Caldas da Rainha, *in 1890* (COI); 1938, *Rothmaler 14098* (LISE). Praia das Macãs near Sintra, 1950, *Rainha 1974* (LISE, UPS). S. Marinho do Pôrto, 1961, *Rainha 5060* (LISE). ALGARCE: Faro, *Guimaraes in 1880, in 1882* (COI). Tavira, *Daveau in 1890* (LISU).

PAKISTAN. West Himalaya, Hazara, *Duthie in 1899* (K); 1963, *Nasir & Siddiqi 1821* (RAW).

INDIA. Punjab, Abbotabad, 1922, *Drummond 20096* (K). Punjab, Manikeru village in valley Parshatti near Kulu, 1934, *Parkinson 3923* (K). Prov. Madhya Pradesh, Balakot, 1959, *Jafri & Ali 3264* (K).

AUSTRALIA. QUEENSLAND: Currumbiu Beach S of Brisbane, *Longman in 1961* (K). Moreton near Southport, 1936, *Pedley 79* (K). Bubya Mountains, 1944, *Clemens 43807* (LIL). South Pine River near Moreton, 1964, *Henderson H97* (K). NEW SOUTH WALES: Bellbrook, *Lengoth in 1891* (MEL-58126). Conjola, *McHeron in 1899* (NSW-135171). Rockdale, *Campfield in 1902* (NSW-135174). Bega, *Tielkens in 1906* (NSW-135172). Tweed Heads, *Cheel in 1916* (NSW-135176). Sussex, *Maiden in 1917* (NSW-135170). Urunga, 1917, *Lawrence 8132-17* (NSW). Warialda, *Gillings in 1920* (NSW-135167). Wondabyne to Woy Woy, *Blakely in 1922* (NSW-135173). Bomaderry, *Rodway in 1936* (NSW-135175). Moura, *Rodway in 1936* (K, NSW-135169). Gearge's Creek, upper Macleay River, *Danis in 1941* (NSW-135180). Grafton, *O'Grady in 1951* (NSW-135178). Kyogle Distr., *Vane in 1958* (NSW-135177). At Manning River near Wingham, 1964, *Salasoo 2820* (NSW). Merriwa, 1970, *Raven et al. 25866* (K, MO, NSW). Bylong, ca. 30 mi NE Mudgee, 800 m, 1970, *Raven et al. 25869* (MO, NSW, PERTH). N Milton on Princess Highway, 1970, *Raven et al. 25894* (K, MO, NSW). Brogo, 12 km N Bega, 1970, *Briggs 3970* (K). 1 mi W Tabulam, 1971, *Salasoo 4609* (NSW). SOUTH AUSTRALIA: Encounter Bay near Port Elliot, 1895, *H. 392* (MEL). WEST AUSTRALIA: Bunbury, *Wickens in 1910* (BM). 25 mi E of Albany, *Elder in 1932* (NSW). Mi Lawley, *Lyon in 1966* (PERTH).

HAWAII. Parker Ranch, 1929, *Carter & Brown 182* (K). Mauna Kea, near pit where David Douglas was murdered, 1949, *Degener et al. 20344* (K, MO).

South Africa. cape: At P.P. Rust, 1905, *Rogers 4117* (PRE). Paarl, 1916, *Smith 2667* (K), 1926, *2667* (K, PRE). Roadside near Faure, Distr. Stellenbosch, 1968, *Parker 4390* (K). transvaal: Nylstroom, 1902, *de Jongh 6529* (PRE). Distr. Pretoria, Scheerport, 1906, *Leendertz 8295* (PRE). Rutzenburg, 1910, *Leendertz 9568* (PRE). Transvaal, *Davy 1248* (PRE). natal: Distr. Durban, Isipingo, 1961, *Ward 3764* (PRE). Distr. Umzinto, Shelley Beach, 1967, *Strey 7281* (K, M, MO, PRE). lesotho: Morija, 1918, *Dieterlen 1352* (P, PRE).

Old specimens from plants cultivated in gardens:

Munich, Germany, Herb. *Zuccarini in 1835* (M; as *O. undulata*). Paris, *in 1835* (P; as *O. chilensis*). Jardin du Luxembourg, *in 1837* (K; as *O. chilensis*). Vienna, Austria, *in 1849*, (W as *O. villosa*).

Oenothera affinis reported in literature from outside of South America:

Portugal: Raven (1968).

South Africa: Ross (1972: 262).

Australia: Bailey (1900: 681; 1913: 215) (as *O. longiflora*); Black (1909: 63; 1926: 427 (as *O. longiflora*); 1952: 638); Beadle et al. (1962: 173).

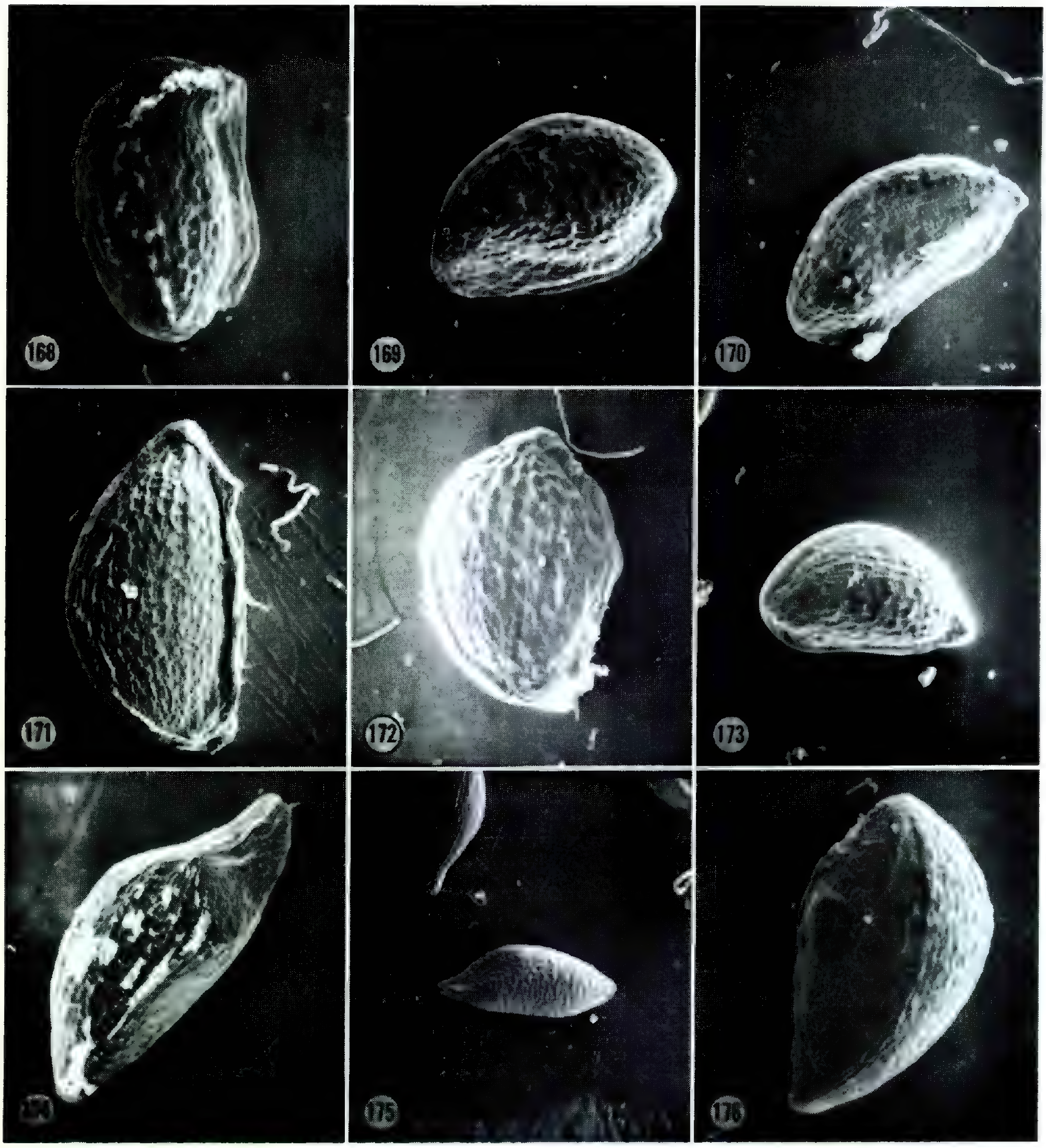
More or less clavate capsules with the valves clearly separate at the apex, a long floral tube, and a dense vestiture of soft pubescence are the most obvious characteristics of *O. affinis*. In comparison with *O. odorata*, the variation is limited. Relatively leafy plants with broad leaves occur throughout the range, especially in the east, but less densely leafy ones in which the leaves are relatively narrow occur only in the northern part of the area of distribution—Bolivia and the provinces of Argentina along the eastern flanks of the Andes.

Just as in *O. odorata*, there are included in *O. affinis* complex heterozygotes which are indistinguishable from the homozygotes of the same species. Both sorts of plants occur in the same populations in *O. affinis*, together with all possible intermediates between 7 pairs and a ring of 14. For example, plants from the vicinity of Tucumán had the following configurations: *Santarius 1672*, ring of 14; *1675*, 7 pairs; *1679*, 7 pairs; *1680*, ring of 6, ring of 4, 2 pairs; *1711*, 7 pairs, another with ring of 4, 5 pairs; *1712*, ring of 8, 3 pairs; *1713*, ring of 6, 4 pairs; *1714*, 7 pairs; *1788*, 7 pairs, another with ring of 4, 5 pairs; *1801*, ring of 8, 3 pairs; ring of 8, ring of 4, 1 pair; *1802*, ring of 4, 5 pairs; *Cleland 425*, 7 pairs. See the general remarks in the introduction on p. 437.

21. **Oenothera mollissima** L., Sp. Pl. 346. 1753.—Figs. 60–62, 134, 182, 219.

Onagra mollissima (L.) Moench, Meth. Pl. 1: 675. 1794.
Oenothera mollissima L. var. *villosa* Sprengel, Pl. Min. Cog. Pug. Prim. 2: 60. 1815. type: not seen.
O. holosericea Tausch, Flora 22: 558. 1839. lectotype: Cultivated in botanical garden, 1836, *J. F. Tausch* (PRC, POM photograph); Munz, Amer. J. Bot. 22: 661. 1935.
Onothera polymorpha H. Lév. race *mollissima* (L.) H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909.
Oenothera mollissima L. var. *genuina* Hassler, Bull. Soc. Bot. Genève, sér. 2, 5: 274. 1913.
Raimannia mollissima (L.) Sprague & Riley, Bull. Misc. Infor. 1921: 201. 1921.

Annual herb, not forming a rosette, the main stem erect or rising obliquely, unbranched or ± well branched, with the side branches arising at right angles or ± obliquely, 3–10 dm tall. Plants densely or very densely and softly long- and short-villous and densely glandular-pubescent. Lower cauline leaves very narrowly elliptic to narrowly elliptic, acute, narrowly cuneate to acute at the base, sessile, 4–7 cm long, 0.5–1.2 cm wide; upper cauline leaves and bracts narrowly oblong to lanceolate, acute, rounded to truncate at the base, sessile; bracts 2–4 cm long, 0.5–1 cm wide, longer than the capsules they subtend, as-



FIGURES 168–176. Scanning electron micrographs of seeds of taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—168. *O. peruana* (Peru, Arequipa, *Santarius 2106*).—169. *O. versicolor* (Peru, Junín, *Santarius 2163*).—170. *O. lasiocarpa* (Argentina, Tucumán, *Diers in 1959*).—171. *O. santarii* (Argentina, Mendoza, *Santarius 1430*).—172. *O. longituba* (Argentina, Tucumán, *Santarius 1736*).—173. *O. scabra* (Bolivia, Cochabamba, *Santarius 2003*).—174. *O. mendocinensis* (Argentina, Buenos Aires, *Santarius 415*).—175. *O. odorata* (Argentina, Río Negro, *Santarius 800*).—176. *O. ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul, *Hackbart in 1966*).

cending and overlapping towards the apex of the stem; leaves plane to strongly undulate along the margins, distantly serrate with blunt teeth. Inflorescence branched. Floral tube (1.5–)2–5 cm long. Buds oblong to lanceolate in outline, green or yellowish green, often red-striped at the junction of the sepals with the floral tube, 0.8–1.5 cm long, 3.5–6 mm thick; apices of the sepals erect, 1–2 mm long. Petals obovate to very broadly obovate, often broadly elliptic, 0.8–2 cm long. Anthers 4–8 mm long. Filaments 7–12 mm long. Style short, the anthers

shedding pollen directly on the stigma at anthesis, 2.5–6 cm long. Stigma lobes 3–5 mm long. Ovary 1–1.3 cm long. Capsule 2.5–3.5 cm long, 3–4 mm thick, often slightly enlarged in upper third. Seeds elliptic in outline, 1.5–2 mm long, 0.7–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 12 and 1 bivalent** at meiotic metaphase I). Flowering time: October–July.

Lectotype: Grown in Cliffort's Garden in Hartekamp, Netherlands, 1735–1737, *C. Linnaeus* (BM; GH and POM photographs). Said to be from the fields of Buenos Aires, Argentina. Linnaeus's diagnosis in the *Species Plantarum* is taken directly from *Viridiarum Cliffortianum* (1737) so the species must be typified by material he had available at that time.

Distribution (Fig. 232): Exclusively in the eastern portion of the range of series *Allochroa*. In Brazil it occurs in the two southernmost states, Santa Catarina and Rio Grande do Sul; in Uruguay, only in the coastal departments of Rocha, Maldonado, Montevideo, Florida, Canelones, San José, and Colonia; in Argentina, it is found in the provinces of Misiones, Corrientes, Entre Ríos, and Buenos Aires.

Specimens examined from cultivated plants:

URUGUAY. MALDONADO: Sandy place in E part of Piriapolis, *Santarius 117*, 118–122, 123*, 124–129* (DUSS; *117, 123* also CTES, M; *117, 118, 123, 128* also MO). Sandy places in S part of Piriapolis, *Santarius 130*, 131–134, 135*, 136–138, 139*, 140–143, 144*, 145, 146, 148, 149, 151* (DUSS; 130, 144, 151 also CTES; *130, 144*, also M; *130, 134, 139, 144, 151* also MO). Dunes E of Piriapolis, *Santarius 157*, 158–173* (DUSS; *157* also M; *157, 166* also MO). Dunes in the W district La Pastora of Punta del Este, *Santarius 174*, 175–185, 186*, 187–191, 192** (DUSS; *174, 186, 192* also CTES, M, MO). Dunes on the coast near Piriapolis, *Krapovickas & Cristobal 11147** (DUSS, MO). MONTEVIDEO: Dunes near Carrasco and Miramar, *Santarius 2*, 3–8, 10, 13*, 14, 16, 19–22, 23*, 24*, 25, 26, 29–31* (DUSS; 2, 13, 23, 24 also CTES; *2, 3, 13, 23, 24* also M, MO). Dunes and pine forest in the Parque F. D. Roosevelt, 3–4 km E of Carrasco, *Santarius 32*, 33–35, 36*, 37, 38, 39*, 40, 41, 42*, 43*, 44–47* (DUSS; *39, 42, 47* also CTES, M; *32, 36, 39, 42, 47* also MO). Carrasco, *Hecht 1964-61** (DUSS). Montevideo, *Hecht 1964-87** (DUSS). Toledo, *Hecht 1964-88** (DUSS). CANELONES: Canelones, *Hecht 1964-25** (DUSS, MO). COLONIA: Sandy place, port of Juan L. Lacaze, *Santarius 48*, 49, 50*, 51–53* (DUSS; *50* also CTES, M; *48, 50* also MO). At roads in W part of Juan L. Lacaze, *Santarius 67** (DUSS). Sandy place in the N part of Juan L. Lacaze, *Santarius 80, 92*, 93–98, 99*, 100, 101** (DUSS; *99, 101* also CTES, M; *94, 99, 101* also MO). Dunes NW of Juan L. Lacaze, *Santarius 102*, 103–108* (DUSS; *102* also MO). FLORIDA: At the railroad 1–3 km NE and SW of Mansavillagra, *Santarius 214**, 221** (CTES, DUSS, M, MO; 214 also SP).

ARGENTINA. CORRIENTES: At Ruta 40 8 km N of Santo Tomé, *Krapovickas & Cristóbal 16406** (DUSS, MO). BUENOS AIRES: Garden of the Botanical Institution of the Faculdad de Agronómia in Buenos Aires, *Santarius 256*, 263, 264, 265*, 266, 267* (DUSS; *256, 265* also CTES, M; *256, 264, 265* also MO). Botanical Garden of Buenos Aires, *Göpel in 1961** (CTES, DUSS, M, MO). Villa Gesell in General Madariaga, *Burkart in 1962** (CTES, DUSS, M, MO).

CULTIVATED: From the main school garden in Frankfurt, Germany, received 1959*, source unknown (CTES, DUSS, M, MO). From the Botanical Garden in Erlangen, received 1960* (CTES, DUSS, M, MO).

Additional specimens examined:

BRAZIL. SANTA CATARINA: Campo de Massiambu near Palhoça, 5 m, *Reitz 4880* (HBR), *Reitz & Klein 1222* (HBR). RIO GRANDE DO SUL: Fazenda Bernardo Velho near Bom Jesus, 1,000 m, *Rambo 34863* (S); between Capão da Canoa and Osório, *Nelson in 1970* (BR); Torres, *Rambo 56194, 54791* (HBR), *Burkart 25105* (SI); city of Rio Grande, *Malme 244, 244a, 270* (S); S. Leopoldo, *Rambo 1283* (LIL); Ilha dos Marinheiros, *Schwacke 2599* (R); Praia de Tramandahy, *Vidal in 1913* (R).

URUGUAY. COLONIA: *N.N. 28* (BAA); Riachuelo, *Cabrera 3340* (NY); Arroyo de Pintos near Puerto Platero, *Bartlett 20771* (GH, MICH, NY, UC); Playa Fomento, *Puerto 1041* (MVFA). SAN JOSÉ: Barra de Sta. Lucía, *Herter 168e* (B); Eifler, *Herter 168g* (US, Z); Playa Pascual, *Arrillaga 742* (MVFA). CANELONES: Toledo, *Herter 168f* (B, GOET, L, SP, Z); Balneario San Luis, *Zorrón 1718* (MVFA, P); Camelon Chico, *Berro 5635* (MVFA); Atlantida, *Osten 21655* (BREM, F, GOET), *Barattini in 1940* (MO); Ruta Interbalneario at km 275, *Lema 6750* (MVFA); Arroyo Sarandi, *Izaguirre 149* (MVFA); El Pinar, *Arrillaga 435* (MVFA); Las Piedras, *Fruchard in 1869* (P); dunes near Floreta, *Steer in 1923* (HBG). MONTEVIDEO: *Rosa-Mato 1509* (LIL), *Isabelle in 1838* (W), *Chabataroff in 1939* (GH), *Gibert 86b, 340, 342* (K), *Gibert 1175* (W), *Gaudichaud in 1839* (G); Carrasco, *Munz 15441* (POM), *15449* (GH, POM), *Felippone 2078* (SI), *Kuhlmann in 1948* (BR); Buceo, *Fruchard in 1875* (P); Playas Blancas, *Fruchard in 1874* (P); Pocitos, *Fruchard in 1876* (NY, RSA, S, SI, US), *Herter 168a* (LE, M, Z), *168b* (G), *76266* (S); Cerro, *Herter 168* (GH, LIL, MO, SI, UC); Punta Gorda, *Rosengurtt B4331* (LIL, MO, MVFA, SP, US); Plata, *Courbon in 1856* (RB); Malvin, *Felippone 2325* (SI), *Herter 168d* (F, HBG, NY). ROCHA: La Paloma, *Descole 174* (LIL); Santa Teresa, *Léon 338* (BAA); La Pedrera, *Rosengurtt 9944a, 9944b* (MVFA), *Hossens 18* (CORD); Cabo Polonio, *Hossens 113* (CORD). MALDONADO: *Berro 3667* (MVFA), *Lourteig 168* (LIL), *Costa 7199* (MVFA); Punta del Este, *Descole 74* (F, GH, LIL, NY); dunes near Solis, *Osten 22389* (S); Cerro Ingles, *Osten 5300* (CORD, SI); Cerro San Antonio near Piriapolis, *Pabst 5496* (HB); San Rafael, *Descole 27* (LIL); Punta Ballenas, *Krapovickas & Cristóbal 12691* (CTES). Department unknown: Road to Lanañaga, *Felippone 2642* (SI).

ARGENTINA. MISIONES: Santa Ana near Candelaria, *Montes 1517* (RSA); road to La Plantadora near San Ignacio, *Scala 258* (LIL); El Dorado near Iguazú, *Schwindt 2231* (LIL); Tapiorny near Cainguas, 215 m, *Schwindt 813* (LIL). ENTRE RÍOS: Concepción del Uruguay, *Lorentz 35* (POM). BUENOS AIRES: *Andersson in 1852* (S), *Rohl 4497* (W); Villa Gesell near Gral. Madariaga, *Boelcke 54* (BAA, MO), *Burkart 22376* (SI); dunes near Pinamar, *Cabrera 10099* (LP), *10674* (LIL, LP); Dock Sur, *Molfino 785* (POM); Isla Paulino, *Cabrera 7384* (F); Punta Lara, *Molfino 247* (POM), *Pujales 54* (LIL); Agua de Oro near Colón, *Dawson 1100* (LP); isle of Martín Garcia, *Moreau in 1933* (RSA); *N.N. in 1949* (SI 26721), *Palacios 35* (LIL); Necochea, *Rodriguez 848* (LIL, S); Jáuregui near Luján, *Burkart 18493* (SI); Juancho near Gral. Madariaga, *Pastore in 1936* (SI 26720), *Cabrera 2715* (LP, NY); San Clemente, *Cabrera 4262, 4271* (LP), *Cabrera 4921* (NY), *Krapovickas 132, 2874* (RSA); *Lourteig 465* (GH, LIL), *Krapovickas 1924* (LIL), *Vervoorst 5208* (BAB); between San Clemente del Tuyú and Mar de Ajó, *Tortosa & Medán 11058* (BAA); Samborobon near Gral. Lavalle, *Haumann 31-1630* (POM); Mar Chiquita, *Lanfranchi 1822* (SI).

Specimens from outside of South America (naturalized):

UNITED STATES. New Jersey, Camden, with ballast, *Martindale in 1866* (GH).

INDIA. Himalaya, cultivated at Almorah, *Duthie in 1900* (K), *Strachey & Winterbottom* (K).

NEPAL. Cultivated (K).

AUSTRALIA. QUEENSLAND: Noosa Heads, *Johnson in 1951* (NSW 135152). NEW SOUTH WALES: N of Raymond Terrace, *Coans in 1961* (NSW 65373); Nelson Bay, *Lithgow in 1965* (NSW 135153); Princess Highway at crossing of Minimurra River, 1 mi S of Albion Park, 1970, *Raven et al. 25887, 25896* (MO, NSW); Centennial Park, Sydney, *Johnson in 1971* (NSW 135154).

Old specimens from plants cultivated in gardens:

Erlangen, Germany, Herb. *Schreber in 1779* (M). Paris, Herb. *Cambessèdes in 1781* (MPU). Vienna, Austria, *in 1806* (W-14035). Schönbrunn at Vienna, *in 1814* (W). Karlsruhe, Germany, *in 1817* (W). Dresden, Germany, *in 1822* (W; as *O. villosa* Thbg.). Munich, Germany, Herb. *Zuccarini in 1832* (M). Munich, *in 1842* (M).

Oenothera mollissima reported in literature from outside its natural area:

VENEZUELA. Pittier et al. (1947: 258; no material seen!); Vareschi (1970: 247–249, fig. 77; the illustration which is said to be *O. mollissima*, represents *O. tetraptera*, Cav., *Oenothera* sect. *Hartmannia*.)

Oenothera mollissima has two chromosomal complexes derived from *O. affinis* but is so different from that species in its small flowers and distinctive habit that it is best regarded as a distinct entity (Tandon & Hecht, 1955, 1956). Hybrids between *O. mollissima* and *O. affinis* or other chromosomally homozygous

species yield progenies in which the two classes of plants differ from one another only trivially, as shown by Haustein (1952). In some strains of *O. mollissima*, both complexes give rise to small-flowered progenies in various combinations; in others, one has genes for a flower size approximating that of *O. affinis*. The small-flowered trait is dominant over the large-flowered one.

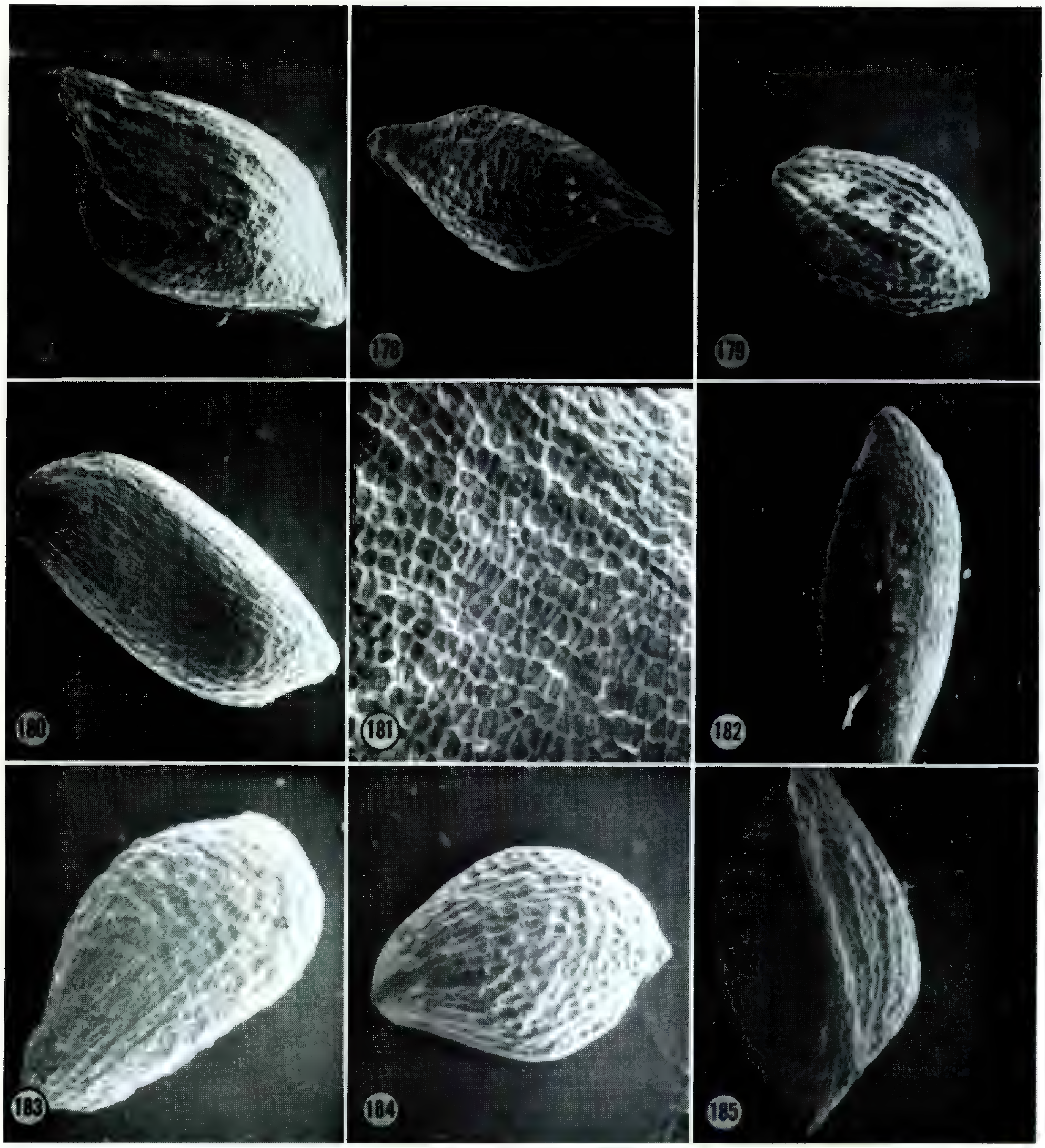
With *O. mollissima* I have included complex heterozygotes (for example, *Santarius 214, 221*) which are, on the basis of their broader leaves and longer floral tube, intermediate to *O. affinis*. Whether such populations have originated by hybridization between the two species and then become stabilized, or actually represent an intermediate stage in the evolution of complex heterozygosity, is not known.

Growing in the same populations as typical *O. mollissima* are often found forms which have apparently originated by introgression with the densely pubescent form of *O. odorata* which occurs in the Province of Buenos Aires. The introgression manifests itself in the lower stature, denser pubescence, undulate leaf margins, and shorter floral tube of these plants. It is not desirable to segregate them taxonomically, however, since they always occur mixed with other plants typical of *O. mollissima* and are best regarded as constituting a part of that species. The very high degree of self-pollination in this species leads to the stabilization of numerous distinctive lines both in the field and in the experimental garden, a veritable feast for the geneticist. Despite this, occasional outcrossing does occur and leads to recombination within the populations, as well as rare interspecific hybridization, which seems to have been of importance in enriching the variability of the species.

22. **Oenothera rivadaviae** Dietrich, sp. nov.—FIGS. 10, 63–64, 135.

Herba ut videtur annua, erecta vel prostrata, rosulata, simplex vel ramis prostratis vel ascendentibus e rosula, caulis principalis 3–7 dm longus. Plantae sparse strigulosae, dense vel sparse villosae, denseque vel sparse glanduloso-pubescentae. Folia rosulae linearia vel angustissime elliptica, acuta, lamina in petiolum gradatim decrescens, 10–15 cm longa, 0.4–0.7 cm lata; folia caulina linearia vel anguste oblanceolata, acuta, basi anguste cuneata vel acuta, sessilia, 4–10 cm long, 0.5–0.8 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi truncata vel subcordata, quam capsulam subtentam longioria vel brevioria, 2–5 cm longa, 0.5–1 cm lata; folia ad margines exigue ad valde undulata, plerumque irregulariter obtuseque serrata. Inflorescentia ramosa. Tubus floralis 1–1.5 cm longus. Gemmae ambito oblongae vel lanceolatae, virides, saepe rubellae, 0.5–1 cm longae, 2.5–4 mm crassae; apices sepalorum divergentes vel erecti, 2–3 mm longi. Petala latissime obovata, 0.6–1.5 cm longa, canarina vel citrina. Stylus brevis, stigmate sub anthesi antheris circumdatus. Ovarium 1.5–2 cm longum. Capsula 3.5–6 cm longa, 2–3 mm lata. Semina ambito anguste elliptica vel elliptica, 1.4–1.8 mm longa, 0.5–0.8 mm crassa. Numerus gameticus chromosomicus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants probably annual, erect or prostrate, forming a rosette, unbranched or with prostrate or ascending side branches from the rosette, the main stem 3–7 dm long. Plants sparsely strigillose, densely or sparsely villous, and densely or sparsely glandular-pubescent. Rosette leaves linear to very narrowly elliptic, acute, gradually narrowed to the petiole, 10–15 cm long, 0.4–0.7 cm wide; cauline leaves linear to narrowly oblanceolate, acute, narrowly cuneate to acute at the base, sessile, 4–10 cm long, 0.5–0.8 cm wide; bracts narrowly lanceolate to



FIGURES 177–185. Scanning electron micrographs of seeds of taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia* (continued).—177. *O. longiflora* subsp. *grandiflora* (Argentina, Corrientes, *Krapovickas & Cristóbal 11293*).—178. *O. indecora* subsp. *indecora* (Uruguay, Maldonado, *Santarius 150*).—179. *O. indecora* subsp. *bonariensis* (Argentina, Buenos Aires, *Santarius 275*).—180. *O. affinis* (Uruguay, Montevideo, *Santarius 193*).—181. *O. affinis* (*Santarius 193*).—182. *O. mollissima* (Uruguay, Montevideo, *Santarius 2*).—183. *O. elongata* (Bolivia, La Paz, *Santarius 2026*).—184. *O. punae* (Argentina, Tucumán, *Santarius 1742*). —185. *O. verrucosa* (Peru, Arequipa, *Santarius 2068*).

lanceolate, acute, truncate to subcordate at the base, longer or shorter than the capsule they subtend, 2–5 cm long, 0.5–1 cm wide; leaves slightly to markedly undulate at the margins, mostly irregularly serrate with blunt teeth. Inflorescence branched. Floral tube 1–1.5 cm long. Buds oblong to lanceolate in outline, green, often flushed with red, 0.5–1 cm long, 2.5–4 mm thick; apices of the sepals divergent or erect, 2–3 mm long. Petals very broadly obovate, 0.6–1.5 cm

long, rich yellow to pale yellow. Anthers 4–6 mm long. Filaments 6–8 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.8–3 cm long. Stigma lobes 4–5 mm long. Ovary 1.5–2 cm long. Capsule 3.5–6 cm long, 2–3 mm thick. Seeds narrowly elliptic to elliptic in outline, 1.4–1.8 mm long, 0.5–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–February.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 18 July 1969. Source: Argentina, Prov. Chubut, gravelly and sandy places in Villa Balneario Rada Tilly, ca. 14 km S of Comodoro Rivadavia, 24 Jan. 1968, *K. A. Santarius 913* (MO-2155717, holotype; DUSS, M, isotypes).

Distribution (Fig. 230): So far known only from a few stations in the provinces of Buenos Aires, Chubut, and Santa Cruz, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Dunes about 2 km SE of Argerich in the research terrain of the Universidad del Sur, 37 km W of Bahía Blanca, *Santarius 401** (CTES, DUSS, M, MO). CHUBUT: Gravelly and sandy places in Villa Balneario Rada Tilly, ca. 14 km S of Comodoro Rivadavia, *Santarius 913*, 918, 923*, 924*, 925*, 930, 935, 936* (DUSS; 923 also CTES; 925 also M; *913, 923, 925* also MO).

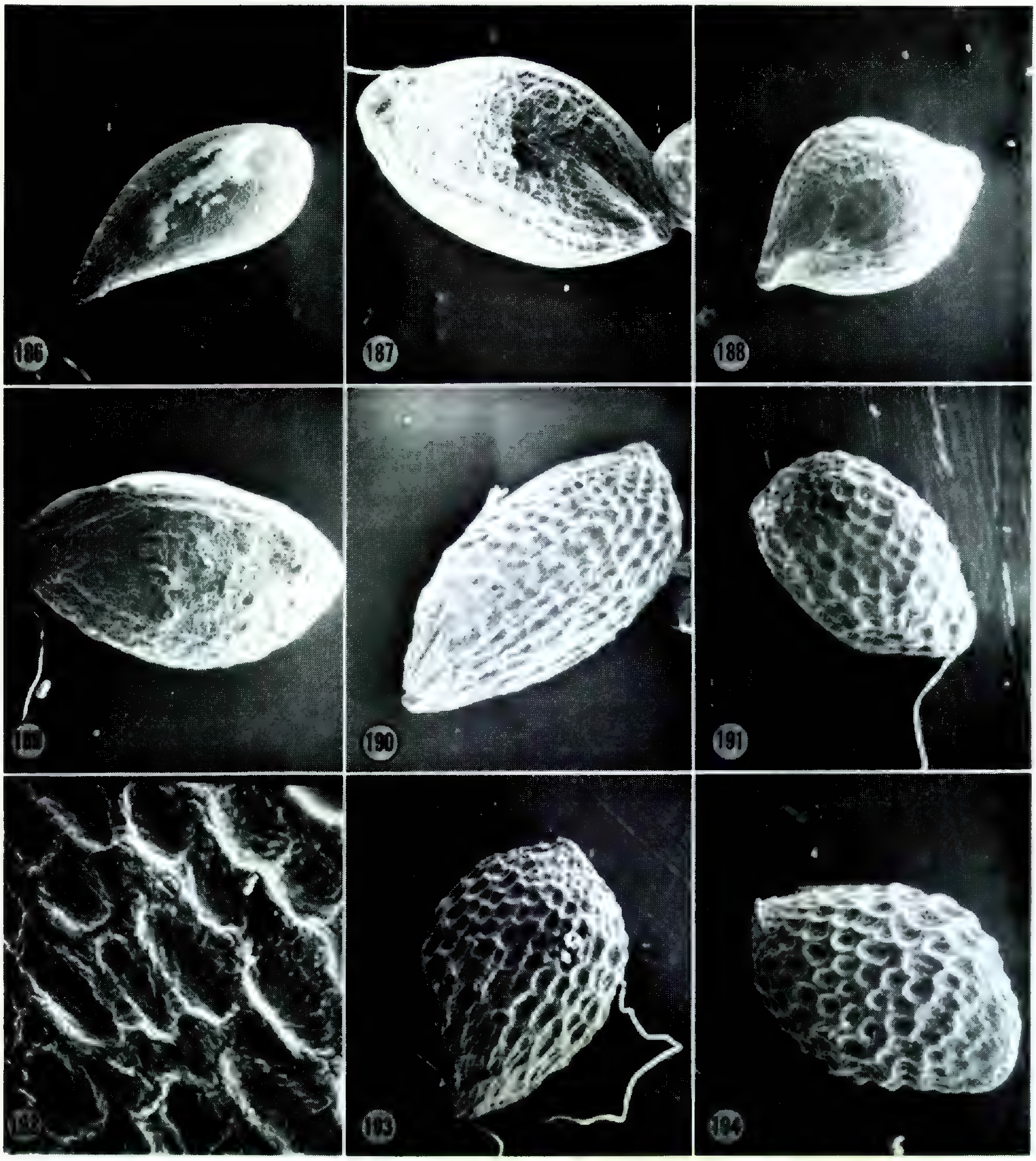
Additional specimen examined:

ARGENTINA. SANTA CRUZ: Comandante Piedrabuena, *O'Donell 3921* (LIL).

Oenothera rivadaviae seems clearly to be a complex heterozygote, the parents of which were *O. mendocinensis* and *O. odorata*. Hybridization with these two homozygous parental species yields plants indistinguishable from them and others indistinguishable from *O. rivadaviae*. The sporadic distribution of this species seems to result from its independent origin following hybridization between its parents at widely separated localities. It may be separated from *O. mendocinensis* by its sparser strigillose pubescence and wider bracts, and from *O. odorata* by its much smaller flowers and narrower capsules.

23. **Oenothera stricta** Ledeb. ex Link ("*striata*"), Enum Pl. Hort. Berol. 1: 377. 1821. H. F. Link misspelled Ledebour's epithet as "*striata*" in publishing the species.—FIGS. 4, 67–72, 136–138, 220–221.

Erect annual or perhaps sometimes biennial herb, rarely decumbent or nearly prostrate, forming a rosette, unbranched or with a branched main stem and side branches arising obliquely or arching upward from the rosette, 3.5–15 dm tall. Plant ± strigillose, especially below, and densely to sparsely long- and short-villous as well as glandular-pubescent. Rosette leaves narrowly elliptic to oblanceolate, acute, gradually narrowed to the petiole or sessile and narrowly cuneate to acute at the base, 10–25 cm long, 0.8–2.5 cm wide; cauline leaves very narrowly elliptic to lanceolate, acute, acute to rounded at the base, sessile, 6–18 cm long, 0.6–2.5 cm wide; bracts narrowly lanceolate to ovate, acute, sessile, truncate to subcordate at the base, 2–3.5 cm long, 0.7–1.5 cm wide, mostly shorter than the capsules they subtend, rarely subequal to them; leaves plane or slightly undulate at the margins, remotely or densely serrate, the teeth blunt or sharp; margins of the bracts usually reddish. Inflorescence simple or branched.



FIGURES 186–194. Scanning electron micrographs of seeds of taxa of *Oenothera* sect. *Oenothera* (continued).—186. *Oenothera coquimbensis* (Chile, Atacama, *Jiles 2160*).—187. *O. arequipensis* (Peru, Arequipa, *Scolnik 1019*).—188. *O. arequipensis* (Peru, Arequipa, *Johnston 3556*).—189. *O. featherstonei* (Peru, Lima, *Macbride & Featherstone 270*). —190. *O. nocturna* (Peru, Lima, *MacHanrish 13*).—191. *O. laciniata* subsp. *pubescens* (Peru, Ayacucho, *Santarius 2235*).—192. *O. laciniata* subsp. *pubescens* (Peru, Junín, *Santarius 2189*). —193. *O. laciniata* subsp. *laciniata* (United States, Missouri, *Russel in 1898*, MO).—194. *O. grandis* (United States, Texas, *Lindheimer 406*, MO).

Floral tube 2–4.5 cm long. Buds narrowly oblong to oblong or lanceolate in outline, green or yellowish green, often flushed with red, 1.2–3 cm long, 0.3–1 cm wide; apices of the sepals erect or divergent, 1–3 mm long. Petals broadly obovate to very broadly obovate, often with a red spot at the base of each one, 1.5–3.5 cm long. Anthers 5–11 mm long. Filaments 10–20 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.8–6 cm long.

Stigma lobes 3–6 mm long. Ovary 1.3–2 cm long. Capsule 3–5 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.3–1.8 mm long, 0.5–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I).

Neotype: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Chile, Prov. Concepción, airport of Concepción, end of 1959, *H. Nodt* (MO-2155718, holotype; CTES, DUSS, M, isotypes).

Distribution (Figs. 230, 231, 235): In Chile from the province of Coquimbo to Isla Chiloe. On the east side of the Andes in the following provinces of Argentina: Neuquén, Río Negro and Chubut, and in the provinces of Chaco, Córdoba, San Luis, and Buenos Aires. The localities for subsp. *stricta* in Ecuador (Quito) and Peru (Lima) must represent stations where the plant is adventive, as is often the case on other continents.

Oenothera stricta has originated as a complex heterozygote between *O. odorata* and *O. ravenii.*

KEY TO THE SUBSPECIES

1. Petals 2.5–3.5 cm long; buds 2–3 cm long, 7–10 mm thick .... 23b. subsp. *altissima*
1'. Petals 1.5–2.5(–3.5) cm long; buds 1.2–1.7 cm long, 3–7 mm thick.
   2. Pubescence shaggy; bracts towards the apex of the stem erect; leaves remotely and bluntly serrate .... 23c. subsp. *argentinae*
   2'. Pubescence not shaggy; bracts towards the apex of the stem spreading; leaves mostly sharply serrate .... 23a. subsp. *stricta*

23a. **Oenothera stricta** subsp. **stricta**.—FIGS. 4, 136, 220.

O. propinqua Spach, Nouv. Ann. Mus. Hist. Nat. 3: 343. 1835. LECTOTYPE: Chile, Prov. Valparaíso, rocky and sandy places along Río Quillota, 1829, *Bertero 1186* (P; LE, NY, P, W, isolectotypes). In his protologue, Spach states that he grew plants from Bertero's seeds, but no corresponding cultivated material has been seen.

O. brachysepala Spach, Nouv. Ann. Mus. Hist. Nat. 3: 345. 1835. TYPE: Chile, Prov. Valparaíso, Quillota, *Bertero 1186* (P, holotype, F and GH, photographs).

O. bracteata Philippi, Anales Univ. Chile 2: 394. 1862. TYPE: Chile, Prov. Curico, Vichuquén near Llico, Dec. 1861, *Landbeck* (SGO, holotype, GH, NY and POM photographs); Linnaea 33: 69. 1864.

O. arguta Greene, Fl. Francisc.: 212. 1891. TYPE: United States, California, Monterey Co., Monterey, July 1891, *Michener* (NDG).

O. propinqua var. *sparsiflora* Philippi, Anales Univ. Chile 84: 631. 1893. TYPE: not located.

O. valdiviana Philippi, Anales Univ. Chile 84: 634. 1893. LECTOTYPE: Chile, Prov. Valdívia, Huchuim, 27 Jan. 1887, *R. A. Philippi* (SGO, holotype, GH, NY and POM photographs).

O. glabrescens Philippi, Anales Univ. Chile 84: 631. 1893. LECTOTYPE: Chile, Prov. Arauco, Lebu, Mar. 1883, *R. A. Philippi* (SGO, holotype, F, GH, NY and POM photographs); Munz, Amer. J. Bot. 22: 661. 1935.

Onagra arguta (Greene) Small, Bull. Torrey Bot. Club 23: 172. 1896.

Oenothera bracteata var. *glabrescens* (Philippi) Reiche, Anales Univ. Chile 98: 476. 1897.

O. mollissima L. var. *valdiviana* (Philippi) Reiche, Anales Univ. Chile 98: 477. 1897; Reiche & Philippi, Fl. Chile 259. 1898.

O. stricta Ledeb. ex Link var. *propinqua* (Spach) Reiche, Anales Univ. Chile 98: 478. 1897; Reiche & Philippi, Fl. Chile 260. 1898.

Onothera polymorpha H. Lév. race *stricta* (Ledeb. ex Link) H. Lév., Monogr. Onoth. 363. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.

O. polymorpha race *propinqua* (Spach) H. Lév., Monogr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.
O. polymorpha race *mollissima* (L.) H. Lév. var. *brachysepala* (Spach) H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909.
Oenothera mollissima subsp. *propinqua* (Spach) Thell., Mitt. Bot. Mus. Univ. Zürich 58: 390. 1912.
O. odorata "Pearce" Cleland, Jap. J. Genet. 43: 332. 1968.

Plants 2.5–10 dm tall, the pubescence not shaggy. Rosette leaves 10–15 cm long, 0.8–1.3 cm wide; cauline leaves 6–10 cm long, 0.6–1 cm wide; bracts 2–3 cm long, 0.7–1.2 cm wide; leaves usually thicker and more sharply serrate than in the other subspecies. Internodes between the capsules 2–4 cm long. Floral tube 2–4.5 cm long. Buds 1.4–1.7 cm long, 3–5 mm thick; apices of the sepal 1–3 mm long. Petals 1.5–2.5(–3.5) cm long. Anthers 7–11 mm long. Filaments 10–20 mm long. Styles 3–6 cm long. Stigma lobes 3–5 mm long. Capsule 3–4 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.4–1.8 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: Northern area, October–May; southern area, October–March.

Distribution (Fig. 230): In Chile from the province of Coquimbo to Isla Chiloé, and on the east side of the Andes only at Lago Nahuel Huapí in the province of Río Negro, Argentina. The localities in Ecuador (Quito) and Peru (Lima) represent escapes from cultivation, as do those on other continents.

Specimens examined from cultivated plants:

CHILE. COQUIMBO: Pisco del Elqui, *Stubbe in 1961** (CTES, DUSS, M, MO). Rivadavia, *Solbrig 3385** (CTES, DUSS, M, MO). VALPARAÍSO: "El Granizo" near Limache, *Göpel in 1961** (CTES, DUSS, M, MO). At the old church in eastern part of Valparaíso, *Göpel in 1961* (CTES, DUSS, M, MO). CONCEPCIÓN: At Río Bío-Bío between Chiguayante and Gualquí, *Mancia in 1965** (CTES, DUSS, M, MO). At Río Bío-Bío near Concepción, *Stubbe in 1960** (CTES, DUSS, M, MO). Airport of Concepción, *Nodt in 1959** (DUSS, M, MO). BÍO-BÍO: Fundo "El Paraíso" near the Monte Aguila, *Göpel in 1962** (CTES, DUSS, M, MO). Los Angeles-Quillaico, *Göpel in 1962** (CTES, DUSS, M, MO). CAUTÍN: Quepe near Temuco, at the railroad near the Río Quepe, *Stubbe in 1960** (CTES, DUSS, M, MO). At the upper current of Río Allipén, on volcanic ashes near Volcán Llaima, *Göpel in 1961** (CTES, DUSS, M, MO). Fundo Walker at Río Trancura N of Volcán Villarica, *Stubbe in 1960** (CTES, DUSS, M, MO). Fundo Saelzer at the S shore of Lago Villarica, *Stubbe in 1960** (CTES, DUSS, M, MO). At Río Allipén SE of Volcán Llaima, *Mittak & Rühm in 1961** (CTES, DUSS, M, MO). VALDIVIA: On dunes near Mehuín, *Nodt in 1959** (CTES, DUSS, M, MO); *Nodt in 1959** (DUSS).

PERU. LIMA: Surco near Lima, *Diers 1091** (CTES, DUSS, M, MO).

*Hecht 1964-8**, source unknown (CTES, DUSS, M, MO). *O. stricta* "Santa Barbara," source unknown, *Cleland 1967-403** (CTES, DUSS, M).

Representative specimens examined:

CHILE. COQUIMBO: Talahueri near Ovalle, *Geisse in 1889* (SGO). ACONCAGUA: Zapallar, *Behn 22800* (CONC). VALPARAÍSO: Quillota, *Philippi in 1856* (W). Between Horcones and Ventana, *Simon 290* (RSA). Limache, *Looser 2008* (GH). Las Zorras, *Harshberger 3391* (NY). Between Curacavi and Casablanca, 600 m, *Killip & Pisano* (RSA, US). Mirasol near Algarrobo, *Kausel 3414* (LIL). Valparaíso, *Sandeman 251* (BM); *Valentín 120* (S); *Maximowitsch 28* (LE); *Mertens* (LD, LE). Río Aconcagua near Caleta de Concón, *Moore in 1884* (SGO). Concón, *Philippi in 1866* (SGO-052879). Viña del Mar, *Philippi in 1882* (BM); *Hicken 263* (SI). Quintero, *Pählmann in 1912* (LD). SANTIAGO: Colina, *Gay 1232* (SGO). San Antonio, *Gay 289* (P); *Valentin in 1921* (S). COLCHAGUA: *Landbeck in 1860* (SGO). CURICO: Cordillera, El Plandion, pass to Argentina, *Bürger in 1903* (GOET). Llico near Vichuquén, *Philippi 613a* (SGO). MAULE: *Kuntze in 1892* (NY). Cauquenes, 1,000–1,650 m, *Ball in 1905* (K). Constitución, *Reiche* (SGO). LINARES: Panimávida, *Philippi in 1885*

(BM); *Holway 224* (US). Longavi, *Schönemann in 1888* (SGO). ÑUBLE: St. Facelco, 520 m, *Pfister 8692* (CONC). Between Curanipe and Buchupureo, *Cox in 1962–1963* (SGO). Hacienda Los Mercedes near Chillán, *Ruiz in 1925* (POM). Puente El Roble near Bulnes, *Parra & Rodriguez 107* (CONC). CONCEPCIÓN: Fundo Trinitaria near Concepción, *Pfister 2166* (CONC). Concepción, *Dombey in 1782* (P); *Neger in 1893–1896* (M); *Jaffuel 3995* (GH); *Mertens* (LE). Hualpén near Concepción, *Barros 6474* (US); *Ricardi 658* (LIL). Río Bío-Bío, *Scott Elliott 86* (BM, NY). Isla Sta. María, *Eights* (US). San Pedro, *Villarod 32162* (CONC). Isla Quiriquina, *Ricardi 10938* (CONC). Coronel, *Ochsenius in 1866* (BR, GOET). Talcahuano, *Hill 162* (K). Lota, *Philippi 610* (SGO). BÍO-BÍO: Fundo Tambillo near Nacimiento, *Pfister 719* (CONC), *186* (LIL). Antuco, *Poeppig in 1829* (M). ARAUCO: Arauco, *Pennell 12920* (F, GH, NY, S, SGO, US). Isla Mocha, *Behn 25366* (CONC). MALLECO: "San Lorenzo" near Angol, *N.N. in 1933* (UC). Mininco, *Schwabe 13338* (CONC). Collipulli, *Ricardi 7455* (CONC). Curacautín, *Burkart 9454* (LIL, SI). Renaico, *Philippi in 1887* (SGO-052830). CAUTÍN: Río Pedregoso near Toltén, *Friedrich 3797* (CONC). Río Zuapa, *Middleton in 1905* (BM). Bajo Imperial, *Middleton in 1906* (BM, G). Gral. Lopez near Temuco, *Sandeman 346* (BM). Temuco, *Claude-Joseph 1843* (US). VALDIVIA: *Philippi in 1888* (K); *Calvert in 1914* (BM); *Buchtien in 1900* (US). San Juan, *Philippi in 1865* (SGO-052881). Niebla near Valdivia, *Buchtien in 1899* (US) (as *O. mollissima* var. *sabulosa* Buchtien). Ranco, *Philippi in 1887* (SGO-052860). Futronhue, *Philippi 613d* (SGO). Cerro Llifén, *Marticorena 63* (CONC); *Boelcke 254* (SI). Bellaviste in the valley of Río Trumas, *Lechler 416* (GOET, K, P). CHILOÉ: Chacao, *Bartulin 12462* (CONC). Isla Chiloé, *Ruiz* (POM); *Nr. 126* (SGO-052883). Castro, *Philippi in 1880* (SGO-052862). Río Palena, *Delfin in 1887* (SGO).

ARGENTINA. RÍO NEGRO: Lago Martín Steffen, *Boelcke 6236* (BAA). Nahuel Huapí, Arroyo Los Cornelios in the valley of Río Limay, *Boelcke & Hunziker 3628* (BAA, MO). BUENOS AIRES: Bahia Blanca, near the port, *Reineck in 1899* (L) (adventive).

ECUADOR. Parque de Ibarra, 2,225 m, 1949, *Solis 13390* (F).

PERU. Rimac valley near Lima, 700 m, 1954, *Rauh-Hirsch 115* (RSA).

Specimens from outside of South America:

UNITED STATES. CALIFORNIA: Monterey Co., *Heller in 1903* (MO).

MEXICO. College garden at Morelia near Michoacán, *Arsène in 1908* (Z).

HAWAII. Maui, Olinda, *Degener in 1927* (MO). Hawaii, Haleakala crater near Holua caves, 1927, *Degener 2254* (K). Haleakala, ca. 2,450 m, 1930, *John 10341* (K); 1940, *Mebold 26664* (M). Kilauea, 1935, *Mebold 20960* (M).

SCOTLAND. Skin works near Selkirk, 1911, *Hayward 1060*, 1913, *1065* (E); 1966, *Webster 10959* (E).

WALES. Aberdovy, *Melville in 1919* (BM), 1919, *Melville 48* (E); 1928, *Britton 3390* (K); 1948, *Taylor 1342* (K). Glamorgan, *Cumming in 1922* (BM, K). SOMERSET: *Duthie in 1869* (BM). Burnham, *Melville in 1873* (E); *Thompson in 1898* (BM, E, K); *Fogitt in 1932* (BM); *Alston in 1949* (BM). Warwick, *Bromwick in 1870* (BM). Berrow, *Davis in 1879* (K); *Fogitt in 1921* (BM).

ENGLAND. BEDFORD: Patton, 1950, *Dony 1221* (K); 1966, *Webster 10942* (E). CHESHIRE: Bickley, *Beer in 1902* (BM). CORNWALL: Gwennap, *Davey in 1903* (E). Par, *Medlin in 1920* (K); *Mebold in 1924* (M). Coverach, *Druce in 1926* (BAS). DEVON: Laira near Plymouth, *Blitt in 1863* (BM). Dawlish Warren, *Redgrove in 1937* (BM); *Proctor in 1952* (LISE). DORSET: Wareham, *Fawett in 1884* (BM); *Linton in 1893* (BM). HAMPSHIRE: Bournemouth, *Alston in 1944* (BM). Blackmoor, 1966, *Webster 10900* (E); 1968, *Lousley 3207*, *3262* (BM). KENT: Catford, *Lowne in 1910* (K). Sandwich Bay, *Meinertshagen in 1932* (BM); *Townsend in 1948* (K); 1961, *Butler 268* (BM). Castle near Sandwich, *Reid in 1975* (BM). Richborough, *Mill in 1860* (K). MIDDLESEX: Twickenham, Clifton Road, *in 1867* (BM). Wandsworth in London, *Forbes in 1837* (BM). NORFOLK: Jarmouth, *Linton in 1879* (BM, K); *Bichham in 1901* (K). SURREY: Croydon, *Bennett in 1873* (E). Bisley Railway, 1958, *Burkill 1639* (E). ISLE OF WIGHT: *Fawett in 1879* (BM); *Jackson in 1894* (K); 1933, *Koster 775* (K); *Townsend in 1951* (K). CHANNEL ISLANDS: Guernsey, *L'Ancresse in 1884* (BM); *Balfour-Brown in 1950* (BM). Jersey, *Watson in 1864* (BM); *Gray in 1894* (BM); 1920, *MacAlister Hall 772* (E); 1954, *Duncan 775* (E).

IRELAND: WEXFORD: Rosslare, *Druce in 1926* (BM).

FRANCE. VIENNE: Châtellerault, *Chabaipeau in 1860* (K, P). LOIRE-ATLANTIQUE: Bourgneuf, *Gad. in 1896* (BM). VENDÉE: Challans, *Portineaux in 1897* (BM). L'Aiguillon, *Foucaud in 1879* (LY); 1911, *Hibon 1461-3* (P). GIRONDE: Bègles, *Neyraut in 1892* (MPU). Pauillac, 1928, *Jallu 461-4* (MPU). LANDES: Capbreton, *Foucaud in 1880* (LY); 1913, *Hibon*

1461-3 (P). Parentis-en-Bors, 1962, *Retz 49626* (LISE). BASSES PYRÉNÉES: St. Jean de Luz, *Barbey in 1883* (Z). Bayonne, 1883, *Blanchet 546* (LISU, LY, MPU, P). Jetée de Boucaud, *Foucaud in 1883* (LY); *Fourés in 1909* (MPU). AVEYRON: Villefranche, *Bras in 1882* (P). HÉRAULT: Castelneau near Montpellier, *Barrandon in 1858, in 1862* (BAS). Sète, *Neyraut in 1887* (MPU); *Cabans in 1933* (MPU). VAR: La Garde-Freinet, Défends du Refrène, 1900, *Bertrand 4725* (HBG, LY, MPO, P), *in 1901* (FR), *in 1903* (LY). Grinaud, *Hibon in 1920* (P). Île d'Aurigny, *Corbière in 1888* (M). MANCHE: Normandie, St. Sauveur-de-Pierrepont, *Corbière in 1893* (LY). FINISTÈRE: Bretagne, *Roscoff, Miciol in 1890* (LY). CHARENTE MARITIME: Montendre, *Foucaud in 1876, 1897 and 1898* (LY). For hybrids with *Oenothera longiflora* subsp. *longiflora* see p. 514.

ITALY. Viareggio, *Ball in 1866* (K); *Caldesi in 1880* (LD); *Lévier in 1882* (P); *Gibelli in 1886* (GOET, LY, MPU); *Mori in 1886* (LD); *Knetsch in 1903* (Z); 1908, *Fiori 1316* (BM, E, K, LY, Z).

PORTUGAL. Figueira, *Mariz in 1882* (COI); 1885, *Goltz de Carvalho 825* (COI, LISE, LISU); *Costa in 1933* (COI); *Silva in 1940* (LISE); *Matos in 1948* (C); 1966, *Reis Moura 706* (COI). Ovar, 1951, *Silva et al. 4563* (LISE); 1966, *Merxmüller & Grau 21497* (M). Caldas da Rainha, *Murray in 1889* (BM). Moita, *da Cunha in 1882* (LISU); *Jorge & Mendez in 1917* (LISU); 1942, *da Silva 140* (LISE); 1954, *Rainha 2762* (LISE); *Fernandes et al. in 1961* (COI, LD). Sintra, 1944, *Rainha 46*, 1950, *1983* (LISE). Martigança, 1956, *da Silva et al. 5727* (LISE). Colares, *da Cunha in 1943* (LISU). Cuitra, *dos Santos in 1909* (LISU). Rocha, *Choffat & Daveaux* (MPU). Mizarella near Guarda, *Ferreira in 1885* (COI). Villar Formoso, *Mariz in 1900* (COI). Marinhais, 1946, *Garcia & Souza 918* (COI).

MADEIRA. Cerro de S. Roque, *Mandon in 1865–1866* (G, K).

SPAIN. Gigón, *Bourgeau in 1864* (C). Lá Coruña, *Guardi in 1888* (BM). San Sebastian near Guipuzcoa, 1895, *Gandoger 186* (C, COI, K). Prov. Gaditana, near Linea de Concepción, 1895, *Porto & Riga 639* (B). Gibraltar, Linea sand hills, *Wolley-Dod in 1912* (BM). Almoreima near Algeciras, 1924, *Ellman & Hubbard 631* (K). Puerto de Santa María near Cadíz, 1929, *Ceballos 2184* (BM, Z); 1968, *Merxmüller & Lippert 23327* (M). Banks of Río Pobones in Andalusia, 1955, *Brinton Lee 87* (BM).

GERMANY. Port of Ludwigshafen, *Zimmermann in 1910* (BAS). Kettwig, *Bonte in 1912* (BAS). Rheinweiler near Basel, Herb. *Fischer* (M).

U.S.S.R. European part of USSR, spontaneous in 1964 in a potato field belonging to the Botanical Garden of the University of Moscow, *Skortsov 10188* (DS, MHA). Not to be regarded as a regular member of the adventive flora of European Russia.

JAPAN. Cultivated, Yokohama, *in 1862* (BM). Kir, 1875, *Rein 20* (GOET). Kyoto, *Rein* (BM, HBG, M); *Hikko in 1877* (HBG). Tokio, Dokwanyama, *Drake in 1881* (P). Harima near Hondo, *Arimoto in 1903* (MO). Kyoto, 1907, *Dunn 8706* (K). Aboshi, 1912, *Schwarz 110* (Z). Honshu, Ashiya, *Fox in 1912* (BM). Kiushu, Hakozaki near Fukada, 1928, *Ichikawa 62* (BM, P). Honshu, Imazu river, 25.6 mi W of Hiroshima, *Charette in 1953* (MO). Niigata, *Drake 52* (P). Yokoka, *Drake* (P).

PAKISTAN. North-West Himalaya, Murree, *Saunders in 1915* (K); 1918, *Stewart 4039* (RAW).

INDIA. Nilghiri, 1840, *Perrotet 408* (P); 1850, *Hohenacker 1146* (K); *Gamble in 1886* (K). Ootacamund near Madras, ca. 2,300 m, 1882, *Brandis 551* (HBG). Punjab, near Banasar, 1885, *Drummond 24435* (K). Punjab, 1922, *Drummond 24434* (K). Himalaya, at the railway between Suni hill and Tulogk, *Rich in 1916* (K). Kashmir, vicinity of Dalhourie, ca. 2,350 m, 1917, *Stewart 2140* (K). Almora, 1,560 m, 1928, *Parker 2021, 2128* (K). Between Kodai Channel and Pulneys, *Bourne in 1898, 1899* (K); *Foreau in 1960* (K).

CEYLON. Roadside near Ambawella, 1932, *Simpson 2577* (BM).

JAVA. 1915, *N.N. 107, 120* (K). Tjibodas, Mt. Pangrango, rare, 3,000 m, 1948, *Djambari 317* (L); 1950, *van Ooststroom 13339* (L).

AUSTRALIA. WESTERN AUSTRALIA: Lower Swan River near Bayswater, *Morrison in 1907* (BM). Bayswater, *Howard 231* (K). Katanning, *Dowell in 1954* (PERTH). Woodman's point, 1961, *Aplin 1071* (PERTH). Claremont, *Steward in 1961* (NSW-135207). Nicholson Road near Cannington, 1961, *George & Marchant 3155* (PERTH). 19 mi SE of Nyabing, 1962, *Newbey 400* (PERTH). Between Borden and Abbany, 1965, *Anway 573* (PERTH). Jerramungup, *Spercer & Fievez in 1971* (PERTH). SOUTH AUSTRALIA: Murrumbidgee, *Nolan in 1841* (MEL). Port Elliot, *Hussey in 1893* (MEL). Mt. Lofty near Adelaide, *in 1897* (MEL). Murray Bridge, *Maiden in 1907* (NSW-135206). Adelaide, *Kaspiew in 1951* (BREM). Wiltunga on Northern York Peninsula, 1966, *Copley 114* (K). Mt. Lofty Range, Balhannah 25 km SE of Adelaide, 1966, *Eichler 18902* (K). Mt. Gambier, 1966, *Wilson 646* (C, MEL).

W shore of Lake Albert, 14 mi W of Meningie, 1967, *Willis 622* (MEL). VICTORIA: Upper Wimmera River near Stawell, *Matthews in 1893* (MEL). Wangaratta, *Weir in 1905* (MEL). Wimmera, *Walter* (MEL-58120). 4 mi NW of Shepparton, between Angustown and Wahoo, *Ackland in 1963* (UPS). 5 mi W of Ararat, 1964, *Muir 3390* (MEL). Red Cliffs, *Henshall in 1964* (MEL). Patchewolluk 11.7 mi N of Hopetoun, 1968, *Belcher 1624* (MEL). NEW SOUTH WALES: Balnarand, 1878, *Lucas 75* (MEL). Filba, *Reader in 1880* (MEL). Riverside near Coonabarralaan, *L. in 1883* (BM). Hume River, *Scott in 1883* (MEL). Turon River, 1885, *Lauterer 40* (MEL). Wagga, *Fletcher in 1888* (NSW-135215). Kogarah, *Campfield in 1893* (NSW-135238). Springfield, 25 mi SW of Cobar, *Andrae in 1895* (MEL-58123). Barbes Creek near Tallong, *Rumsey in 1898* (NSW-135240). Jenolan Caves, *Blakely in 1900* (NSW-135231). Orange, *Boorman in 1906* (NSW-135236). Bega, *Ziethen in 1906* (NSW-135228). Richmond, *Carne in 1906* (NSW-135242). Blackheath, *Maiden in 1908* (NSW-135233). Emu plains, *Hamilton in 1912* (NSW-135241). Wallendbeen, *Beakwell in 1913* (NSW-135219). Bathurst Farm, *Noble in 1914* (NSW-135235); *Brett in 1914* (NSW-135234). Hill Top, Southern Line, *Cheed in 1915* (NSW-135237). Tinga, *Boorman in 1917* (NSW-135222). Blue Mountain, *N.N. in 1919* (MEL-58109). Rylstone, 1920, *Morton 5865-20* (NSW). Tumut, *Redford in 1921* (NSW-135214. Cocketgedong near Jerilderie, *Sibb in 1921* (NSW-135224). Wondabyne to Woy Woy, *Blakely in 1922* (NSW-135243). Junee Distr., *Nugent in 1923* (NSW-135216). Harden, *Rodway in 1924* (NSW-135218). Wallangra, *Rodway in 1929* (NSW-135223). Cullerin, 25 mi W of Goulburn, *Simpson in 1935* (NSW-135229). Armidale University Grounds, *Davis in 1941* (NSW-15230). Morivale to Wellington, *Shelley in 1946* (NSW-135212). Narrabeen Lake, *Johnson in 1946* (NSW-135239). Carlaminda, *Castin in 1948* (NSW-135227). Near Wellington, *Dunk in 1950* (MEL-58103). Narrhari, *Moore in 1952* (NSW-134226). Albury distr., *Glenfield in 1953* (NSW-135213). Near Kootingal, 8 mi ENE of Tamworth, 1954, *Kelso & Goode 64* (NSW-135220). Menindee, *Constable in 1955* (K, MO, NSW-38446). Near Wyong, 1958, *Salasoo 1633* (NSW). Cowro Research Station, *Hill in 1960* (NSW-135210). Canberra, 1962, *Mukee 9666* (NSW). Cootamundra, *Francis in 1963* (NSW-135217). Narrandera, *Leeton in 1963* (NSW-135225). Gunnedah Distr., *Beeson in 1964* (NSW-135221). Michelago to Williamsdale, *Salasoo in 1969* (NSW). Bylong, 33 mi NE of Mudgee, 800 m, 1970, *Raven et al. 25868* (MO, NSW). Pinch River, 39 mi SSW of Jindabyne, 1970, *Pickard & Coveny 2758* (MEL, NSW). QUEENSLAND: *Caves in 1874* (MEL). Silverwood, 1922, *White 1735* (NSW-135209). Mt. Playfair station near Leichhardt, 1964, *Adams 1352* (K). Maryland, *Hickey in 1884* (MEL). Boxbill, *Reader in 1884* (MEL). Lilliput, *in 1913* (MEL). Near Klunzy, *Mueller* (MEL-58115). TASMANIA: Hobart, *Lucas in 1913* (NSW-135208).

NEW ZEALAND. Roturoa, *Chase et al. in 1909* (BM, LIL, K, MO). Swamp near head of Rangaunu, harbour of Puheke Hill, *Mason & Moar in 1949* (AI). Sulphur Springs Bay near Rotoity, *Hurvey in 1949* (AI). Owairaka Park Domain, *Wood in 1950* (AI). Coal Creek, 90 Mile Beach, *Cooper in 1966* (AI). Murimotu at North Cape, *Adams in 1968* (AI). New Zealand, *Hooker in 1870* (K). Paumure, *TFC* (AI).

LIBYA. Distr. Tripolis, Sidi Mesri, 50 m, 1960, *Keith 827* (K).

EGYPT. Near a small village at the Channel *in 1872* (BM).

RHODESIA. Salisbury, on railway, ca. 1,650 m, 1919, *Eyles 1533* (BM, SRGH). Distr. Mtoko, ca. 1,000 m, 1956, *Davies 1926* (K, SRGH). Melsetter village, 1968, *Goldsmith 126-68* (M, SRGH); 1960, *Phipps 2844* (SRGH).

MOZAMBIQUE. Inhaça Island, 23 mi E of Lourenço Marques, 1959, *Mogg 31640* (K).

SOUTH AFRICA. CAPE: Loerie, 1894, *Penther 2150* (M). Distr. Aliwal North, Kraai River, ca. 1,450 m, 1933, *Gerstner 198* (PRE). Distr. East London, 1960, *Comins 2038* (PRE). Distr. Alexandria, Reed Valley, ca. 320 m, 1953, *Archibald 5886* (PRE). Distr. Humansdorp, 1921, *Fourcade 1762* (K). Somerset, *Bowhen* (K). Stellenbosch, 1948, *Parker 4391* (K). Rondebosch, 1934, *Adanson 2232* (BM). TRANSVAAL: Woodbush, 1909, *Jenkins 7201* (PRE). Bokfontein, 1909, *Jenkins 7542* (PRE). Witzies Hoek, 1917, *Junod 14522* (PRE). Grahamstown, 1918, *van Dam 18837* (PRE). Knysna, 1921, *Breyer 23334* (PRE). Along railway near Benoni, 1934, *Bradfield 189* (PRE). Pretoria, 1936, *Reptar 650* (PRE). Bethlehem, *Potgieter 21840* (PRE). ORANGE FREE STATE: Clarence, 1917, *Van Hoepen 18172* (PRE). Gansfontein near Ficksburg, ca. 1,750 m, 1934, *Galpin 13877* (K, PRE). Doornhoek near Bloemhof, *Botha in 1936* (PRE-29489). Bloemfontein, 1951, *Gemmell 6142* (K, PRE); *Hanekom 811* (K, SRGH); 1951, *Potts 6142* (K). *Natal*: 1902, *N.N. 41* (BM). LESOTO: Distr. Tebetebeng, 1957, *Jacot-Guillarmod 2928* (PRE). Maseru, ca. 1,650 m. 1970, *Williamson 19* (K). Leribe, *Dieterlen 169* (P). Province unknown: Wit pootje Kloof, 1948, *Moss 4648* (BM).

Hybrids between *O. stricta* subsp. *stricta* and *O. indecora* subsp. *bonariensis* occur in Australia and Portugal, and are cited under *O. indecora* (p. 522).

Early specimens from plants cultivated in gardens:

Botanical Garden of Dresden, Germany, *Bauer in 1819* (CORD). Copenhagen, Herb. 1820, *Schum. 18* (C). Copenhagen, Herb. 1822, *Schum. 26* (C; as *O. fraseri*). Copenhagen, Herb. 1822, *Schum. 25* (C; as *O. salicifolia*). Botanical Garden of Frankfurt, Germany, seeds from Berlin, *Becker in 1825* (FR; as *O. striata*). Paris, *in 1842* (BR). Leningrad, *in 1848* (LE). Vienna, Austria, *in 1849* (W; as *O. chilensis*).

Oenothera stricta subsp. *stricta* reported in literature from outside of South America:

ENGLAND. Trimen & Dyer (1869: 111, as *O. odorata*); Babbington (1881: 136, as *O. odorata*); Murray (1896: 154, as *O. odorata*); Hanbury & Marshall (1899: 158, as *O. odorata*); Linton (1900: 105, as *O. odorata*); Marquand (1901: 363, as *O. odorata*); Lester-Garland (1903: 113, as *O. odorata*); Davey (1909: 203, as *O. odorata*); Trow (1911: vol. 1: 71, as *O. odorata*); Hooker (1930: 158, as *O. odorata*); Dony (1953); Butcher (1961: vol. 1: 798); Clapham et al. (1962: 480); Perring & Walters (1962).

FRANCE. Gandoger (1886: 49); Corbière (1894: 239); Burnat (1899: vol. 3: 198); Rouy & Camus (1901: 201); Coste (1903: vol. 2: 81); Thellung (1912, as *O. mollissima* subsp. *odorata*); Bonnier (1921: vol. 4: 29); Chassagne (1957: vol. 2: 160); Issler et al. (1965: 357); Raven (1968).

GERMANY. Raven (1968).

BELGIUM. Jean (1975).

SWITZERLAND. Raven (1968).

PORTUGAL. Coutinho (1913: 426; 1939: 508); Sampaio (1946: 408); Raven (1968).

SPAIN. Willkomm & Lange (1880: 181); Willkomm (1893: 219); Colmeiro (1886: vol. 2: 389); Menezes (1914, as *O. odorata*); Wolley-Dod (1914: 42; 1949: 40).

ITALY. Arcangeli (1882: 238); Gandoger (1886); Fiori & Paoletti (1899: vol. 2: 134); Saccardo (1909: 176); Fiori (1925: vol. 2: 14). Zangheri (1976: vol. 1: 421).

U.S.S.R. Shteinberg (1949: 630; 1974, Engl. transl.: 472, as *O. odorata*); Raven (1968)[4].

MOROCCO. Jahandiez & Maire (1931: 516).

ALGERIA. Quézel & Santa (1963: 639).

ETHIOPIA. Bizzari & Raven (1972: 469).

SOUTH AFRICA. Adamson & Salter (1950: 606); Guillarmod (1971: 215, as *O. longiflora*); Ross (1972: 262).

INDIA. Graham (1839: 75, as *O. mollissima*); Hooker (1879: vol. 2: 582, as *O. odorata*); Fyson (1915: vol. 1: 161, vol. 2: 116, as *O. odorata*); Trimen (1931: 131, as *O. odorata*).

CEYLON. Trimen (1894: 235, as *O. odorata*).

JAPAN. Makino (1949: 290, *tab. 868*).

CHINA. Iconographia (1972, as *O. odorata*).

AUSTRALIA. Black (1909: 63; 1926: vol. 3: 427, as *O. odorata*; 1952: vol. 3: 638); Beadle et al. (1962: 173, as *O. odorata*); Eichler (1965: 243).

NEW ZEALAND. Kirk (1899: 180, as *O. odorata*); Cheeseman (1925: 1073).

UNITED STATES. Munz (1965).

The stations for this subspecies at Lago Nahuel Huapí and the Río Limay in Argentina might represent introductions, like those in Ecuador and Peru, especially since there is a constant flow of tourists from Chile to the national parks in Argentina.

This subspecies is morphologically similar to *O. ravenii* subsp. *chilensis*, itself an entity which includes genes from the other parent of *O. stricta*, *O. odorata*. *Oenothera stricta* can be distinguished from *O. ravenii* subsp. *chilensis*, however, by its longer bracts and less erect habit. In fact, considering the range of variation in the species as a whole, the epithet "*stricta*" is a little unfortunate,

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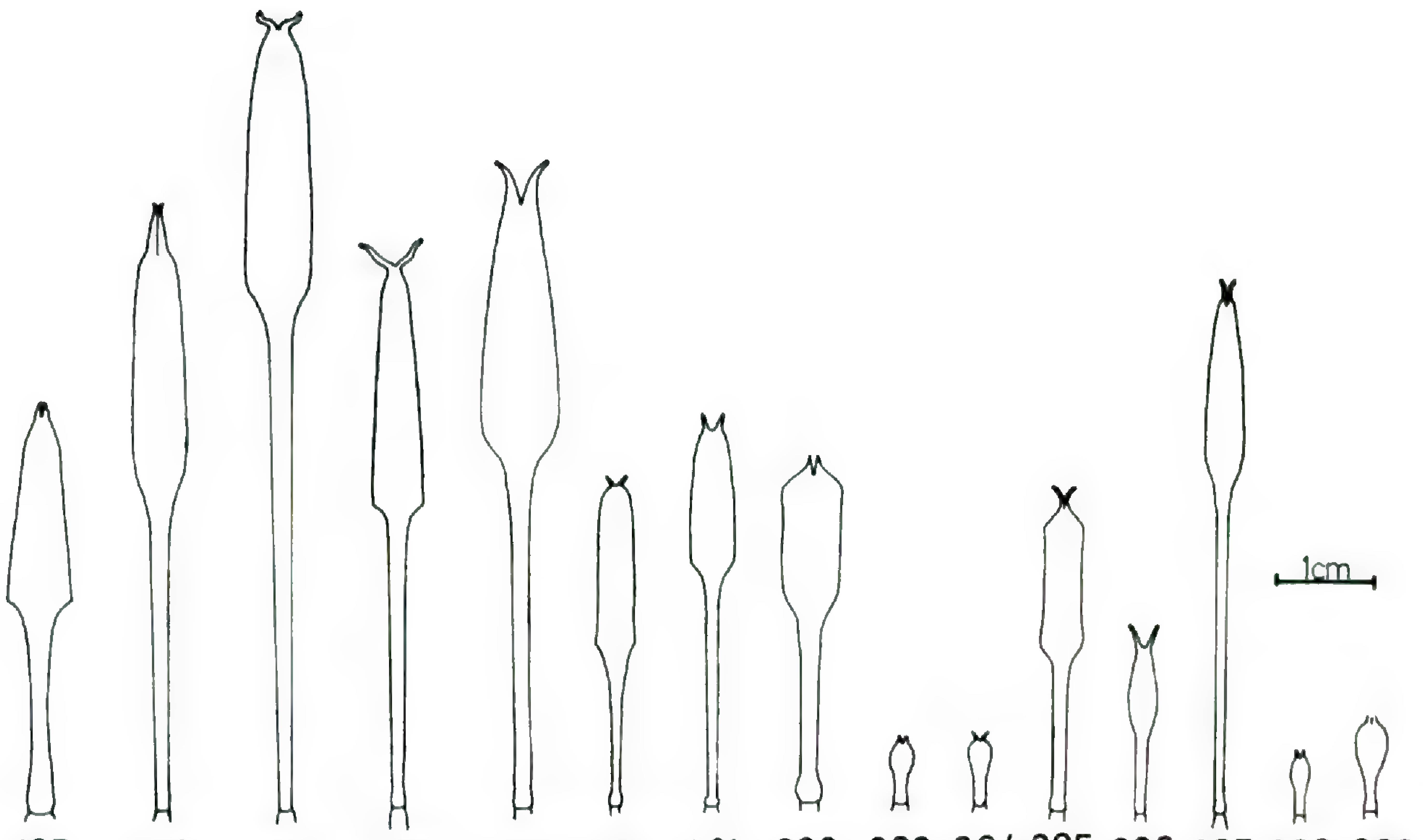
[4] A. K. Skvortsov has kindly informed us that the specimen (*Skvortsov 10188*, DS, MHA) on which Raven (1968) based his record from European Russia was from adventive plants which appeared only in 1964. The species is naturalized in the vicinity of Vladivostok.



Figures 195–209. Schematic outlines of buds of taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—195. *O. santarii* (Argentina, Mendoza, *Santarius 1495*).—196. *O. longituba* (Argentina, Tucumán, *Santarius 1736*).—197. *O. longituba* (Argentina, Jujuy, *Fabris 5787*).—198. *O. pedunculifolia* (Argentina, Tucumán, *Santarius 1781*).—199. *O. scabra* (Bolivia, Cochabamba, *Santarius 2003*).—200. *O. scabra* (Peru, Ayacucho, *Santarius 2251*).—201. *O. sandiana* (Peru, Cuzco, *Santarius 2269*).—202. *O. sandiana* (Peru, Junín, *Santarius 2132*).—203. *O. nana* (Peru, Puno, *Santarius 2058*).—204. *O. nana* (Peru, Puno, *Santarius 2055*).—205. *O. villaricae* (Chile, Valdivia, *Göpel in 1961*).—206. *O. cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—207. *O. acuticarpa* (Argentina, Tucumán, *Göpel in 1961*).—208. *O. punae* (Argentina, Tucumán, *Santarius 1742*).—209. *O. verrucosa* (Peru, Arequipa, *Santarius 2073*).

since there are decumbent or nearly prostrate dune and strand forms, such as *Nodt in 1959*.

Especially in the northern part of the range, in the provinces of Coquimbo and Valparaíso, plants with a relatively long floral tube (4–4.5 cm) are frequent (e.g., *Göpel in 1961*, Valparaíso). They correspond more or less to the type of *O. brachysepala* Spach. The most likely explanation for the origin of these plants seems to be introgression from *O. affinis*, either directly or via *O. picensis*, which contains one complex from *O. affinis* and like it grows with *O. stricta* in northern Chile.

23b. **Oenothera stricta** subsp. **altissima** Dietrich, subsp. nov.—Figs. 67–69, 137, 221.

Plantae 5–15 dm altae; pubes non hirta. Folia rosulae 10–20 cm longa, 1.2–1.7 cm lata; folia caulina 7–15 cm longa, 1–17 cm lata; bractea 2–3.5 cm longa, 0.5–0.7 cm lata; folia remote obtuseque serrulata. Internodia inter capsulas 4–5 cm longa. Tubus floralis 2.5–3.5 cm longus. Gemmae 2–3 cm longae, 7–10 mm crassae; apices sepalorum 1–3 mm longi. Petala 2.5–3.5 cm longa. Capsula 3.5–5 cm longa, 3–4 mm crassa. Semina ambito late elliptica, 1.5–1.8 mm longa, 0.6–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 5–15 dm tall, the pubescence not shaggy. Rosette leaves 10–20 cm long, 1.2–1.7 cm wide; cauline leaves 7–15 cm long, 1–1.7 cm wide; bracts 2–3.5 cm long, 0.5–0.7 cm wide; leaves remotely serrate, with dull teeth. Internodes between the capsules 4–5 cm long. Floral tube 2.5–3.5 cm long. Buds 2–3 cm long, 7–10 mm thick; apices of the sepals 1–3 mm long. Petals 2.5–3.5 cm long. Anthers 6–7 mm long. Filaments 13–18 mm long. Style 3.5–5 cm long. Stigma lobes 3.5–6 mm long. Capsule 3.5–5 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.5–1.8 mm long, 0.6–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–March.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 11 Aug. 1972. Source: Argentina, Prov. Río Negro, NW slopes at Ruta 258 ca. 3 km N of Río Villegas (67 km S of San Carlos de Bariloche), on volcanic ashes and marl, 700 m, 19 Jan. 1968, *K. A. Santarius 798* (MO-2155212, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 231): Along the eastern side of the Andes at low elevations in the provinces of Neuquén, Río Negro, and Chubut, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. PROV. RÍO NEGRO: NW slopes at Ruta 258 ca. 3 km N of Río Villegas, 700 m, *Santarius 798**, *799** (DUSS, MO; *798* also M). N slopes at Ruta 258, 1.5 km S of Río Villegas, on volcanic ashes and marl, 550 m, *Santarius 800** (DUSS, M, MO).

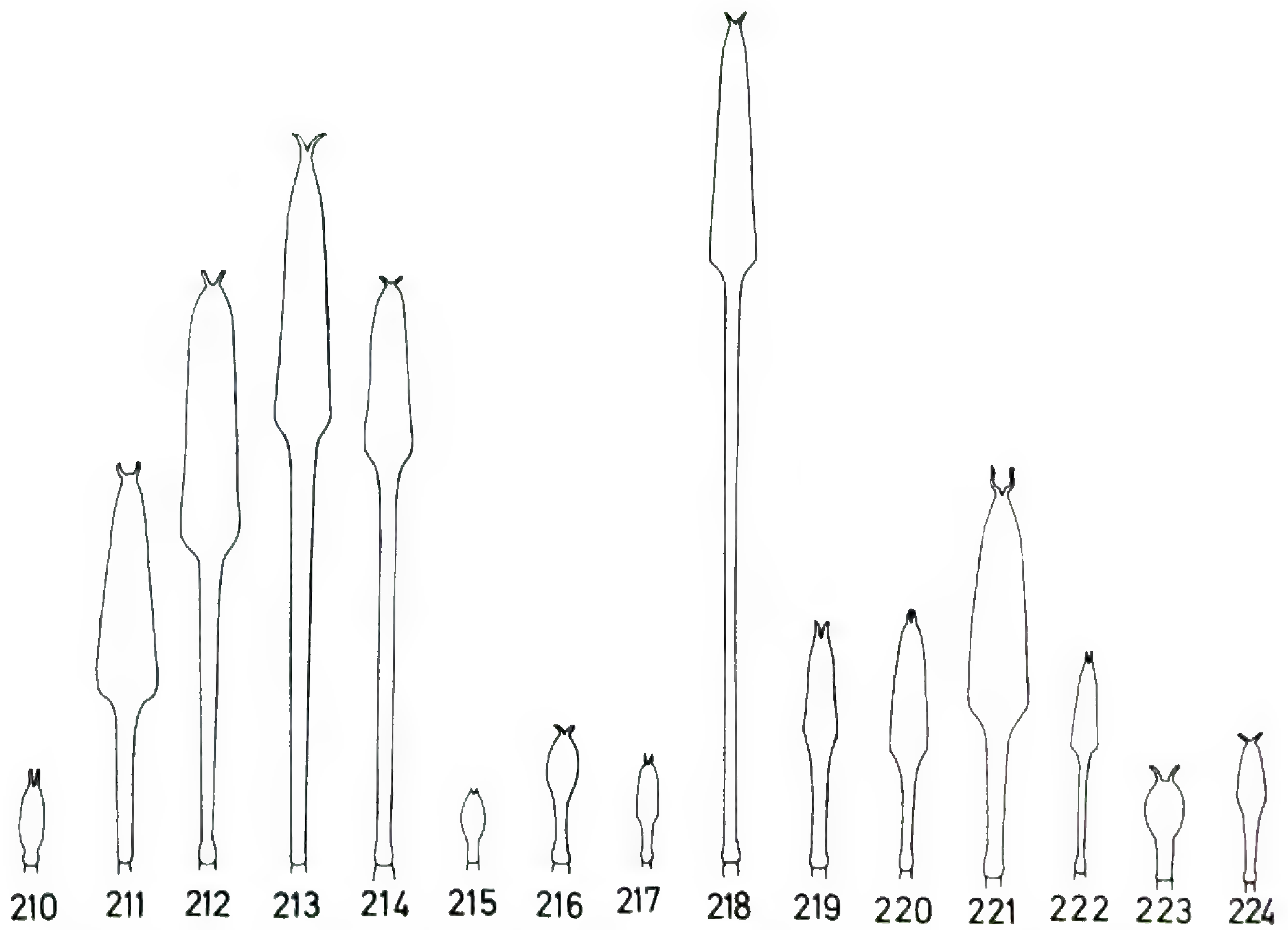
Additional specimens examined:

ARGENTINA. NEUQUÉN: Cascada Maipú, *De Barba 1839* (LIL). Lago Lolog, *De Barba 1794* (LIL). Aluminé, *Soriano 1272* (BAB). Lago Epulafquén, *Dawson & Schwabe 2456* (BAB). San Martín de los Andes, *De Barba 1694* (LIL); *O'Donell 2373* (LIL, NY), *2415* (LIL); *Eskuche 01329* (CTES). Quila Quina, *Cabrera 20521* (LP, P); *Achajonsky 3399* (BAB). Lago Nonthué, Hua Hum, *Valla et al.* (MO). Chos Malal, ca. 650 m, *Comber 169* (K). RÍO NEGRO: S.C. de Bariloche, *De Barba 322* (LIL). Cerro Granito near Bariloche, *Meyer 8244* (LIL). At Ruta 258 near Río Foyel, *Dawson 3290* (BAB, LP). Villegas, *Lourteig & Buchinger 201* (P); *Moreau in 1941* (RSA). El Bolsón, *Meyer 7884* (LIL). CHUBUT: Epuyén near Cushamén, *Muniez 5504* (BAB). Río Corcovado, *Illin 147* (UC).

Considering the relatively large size of its flowers, *O. stricta* subsp. *altissima* may be at an earlier stage in the evolution of complex heterozygosity than is subsp. *stricta*. Since the influence of *O. odorata* is predominant in the phenotype of *O. stricta* subsp. *altissima*, one could assume that this entity arose from the combination of a chromosomally homozygous strain of *O. odorata*, common in the right area, with a genome of *O. ravenii* introgressed with *O. odorata*, the latter probably by way of the Chilean subspecies of *O. stricta*. The direct combination of *O. odorata* with the homozygous, large-flowered *O. ravenii* seems very unlikely, especially since the two are not known to grow together anywhere.

23c. **Oenothera stricta** subsp. **argentinae** Dietrich, subsp. nov.—FIGS. 70–72, 138.

Plantae 5–13 dm altae; pubes hirta. Folia rosulae 10–25 cm longa, 1.5–2.5 cm lata; folia caulina 7–18 cm longa, 0.8–2.5 cm lata; bractea 2.5–3.5 cm longa, 0.7–1.5 cm lata, ad apicem caulis aliquantum imbricata; folia remote obtuseque serrata. Internodia inter capsulae 1.5–3 cm longa. Tubus floralis 2–3.5 cm longus. Gemmae 1.2–1.5 cm longae, 5–7 mm crassae; apices sepalorum 1.5–2 mm longi. Petala 1.5–2 cm longa. Capsula 3–4 cm longa, 3–4 mm lata.



FIGURES 210–224. Schematic outlines of buds of taxa of *Oenothera* sect. *Oenothera* subsect. *Munzia*.—210. *O. mendocinensis* (Argentina, Buenos Aires, *Santarius 411*).—211. *O. odorata* (Argentina, Neuquén, *Santarius 624*).—212. *O. ravenii* subsp. *ravenii* (Brazil, Rio Grande do Sul, *Hackbart in 1966*).—213. *O. longiflora* subsp. *grandiflora* (Argentina, Corrientes, *Krapovickas & Cristóbal 11293*).—214. *O. longiflora* subsp. *longiflora* (Uruguay, Colonia, *Santarius 82*).—215. *O. indecora* subsp. *indecora* (Uruguay, Florida, *Santarius 212*).—216. *O. indecora* subsp. *indecora* (Uruguay, Florida, *Santarius 205*).—217. *O. indecora* subsp. *bonariensis* (Botanical Garden Erlangen).—218. *O. affinis* (Argentina, Jujuy, *Santarius 1851*).—219. *O. mollissima* (Uruguay, Montevideo, *Santarius 32*).—220. *O. stricta* subsp. *stricta* (Chile, Concepción, *Stubbe in 1960*).—221. *O. stricta* subsp. *altissima* (Argentina, Río Negro, *Santarius 800*).—222. *O. picensis* subsp. *cordobensis* (Argentina, Córdoba, *Göpel in 1961*).—223. *O. parodiana* subsp. *parodiana* (Uruguay, Florida, *Santarius 207*).—224. *O. nocturna* (Peru, Lima, *Santarius 2333*).

Semina ambito late elliptica, 1.3–1.5 mm longa, 0.6–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 5–13 dm tall, the pubescence shaggy. Rosette leaves 10–25 cm long, 1.5–2.5 cm wide; cauline leaves 7–18 cm long, 0.8–2.5 cm wide; bracts 2.5–3.5 cm long, 0.7–1.5 cm wide, overlapping to a considerable extent towards the apex of the stem; leaves remotely serrate, with blunt teeth. Internodes between the capsules 1.5–3 cm long. Floral tube 2–2.5 cm long. Buds 1.2–1.5 cm long, 5–7 mm thick; apices of the sepals 1.5–2 mm long. Petals 1.5–2 cm long. Anthers 5–7 mm long. Filaments 10–12 mm long. Style 2.8–3.7 cm long. Stigma lobes 3–6 mm long. Capsule 3–4 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.3–1.5 mm long, 0.6–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Buenos Aires, E end of the Sierra del Volcán NW of Puerta El Abra, at km 45 of Ruta 226 between Mar de la Plata and Balcarce, partly grazed terraces between rocks, 150–300 m, 7 Jan. 1968, *K. A. Santarius 346* (MO-2155215, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 235): Known only from a few localities in the provinces of Chaco, Córdoba, San Luis, and Buenos Aires, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: E end of the Sierra del Volcán, at km 45 of Ruta 226 between Mar de la Plata and Balcarce, 150–300 m, *Santarius 346**, *347*, *348*, *350–354*, *355**, *356–367*, *368** (DUSS; *355*, *368* also CTES; *346*, *355* also M; *346*, *352*, *355*, *358*, *368* also MO).

Additional specimens examined:

ARGENTINA. CHACO: Colonia Benítez, *Schulz 792* (POM). Las Palmas, *Jörgensen 2487* (LIL). CÓRDOBA: La Isla near Santa María, *de la Sota 708* (LIL). La Falda near Punilla, *Stuckert 4323* (CORD). Casa Grande near Punilla, *de la Sota 3411* (LIL). Cruz Grande near Punilla, *de la Sota 3634* (LIL). SAN LUIS: Paucanta, *Castellanos 25-864* (POM). BUENOS AIRES: S. Vigilancia near Balcarce, *Jurado 140* (LIL).

This subspecies can be distinguished from the other two by its shaggy pubescence, a characteristic that is often found in *O. ravenii.* The inflorescence of this subspecies is more crowded than in the others, and the internodes between the capsules shorter. It is more heavy-set than in the other subspecies, with the thicker stems and broader leaves especially prominent. In all of these respects, *O. stricta* subsp. *argentinae* approaches *O. ravenii*, which predominates in its genetic makeup in the same way that *O. odorata* does in that of *O. stricta* subsp. *altissima*, a relationship that can easily be understood on geographical grounds.

24. **Oenothera bahia-blancae** Dietrich, sp. nov.—FIGS. 73–75, 139.

Herba annua erecta, rosulata, simplex vel caulis principalis ramosus et ramis oblique e rosula ascendentibus, 5–8 dm alta. Plantae dense vel sparse strigulosae, pilis brevibus longibusque sparse praeditae, et sparse glanduloso-pubescentes. Folia rosulae anguste oblanceolata, acuta, lamina in petiolum gradatim decrescens, 10–15 cm longa, 0.5–1.2 cm lata; folia caulina anguste elliptica vel anguste lanceolata, acuta, sessilia, basi anguste cuneata vel acuta, 5–10 cm longa, 0.6–1.5 cm lata; bractea anguste lanceolata vel lanceolata, acuta, sessilia, basi rotundata vel truncata, 2–3 cm longa, 0.7–1 cm lata; folia plana vel ad margines undulata, irregulariter obtuseque serrata. Inflorescentia simplex vel ramosa. Tubus floralis 1.2–2.5 cm longus. Gemmae ambito oblongae vel lanceolatae, virides vel flavovirescentes, saepe junctura sepalorum tubo florali rubrofasciatae, 0.6–1.2 cm longae, 3–4 mm latae. Sepala saepe fusco-rubro punctata; apices sepalorum erecti, 1–2 mm longi. Petala obovata vel latissime obovata, 0.7–1.5 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.3–1.5 cm longum. Capsula (2–)3–4.5 cm longa, 3–4 mm crassa. Semina ambito late elliptica, 1.2–1.5 mm longa, 0.6–0.8 mm crassa. Numerus gameticus chromosomicus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, forming a rosette, with a simple or branched main stem and the side branches arising obliquely from the rosette, 5–8 dm tall. Plants densely to sparsely strigillose, sparsely long- and short-villous, and sparsely glandular-pubescent. Rosette leaves narrowly oblanceolate, acute, gradually narrowed to the petiole, 10–15 cm long, 0.5–1.2 cm wide; cauline leaves narrowly elliptic to narrowly lanceolate, acute, sessile, narrowly cuneate to acute at the base, 5–10 cm long, 0.6–1.5 cm wide; bracts narrowly lanceolate to lanceolate, acute, sessile, rounded to truncate at the base, 2–3 cm long, 0.7–1 cm wide;

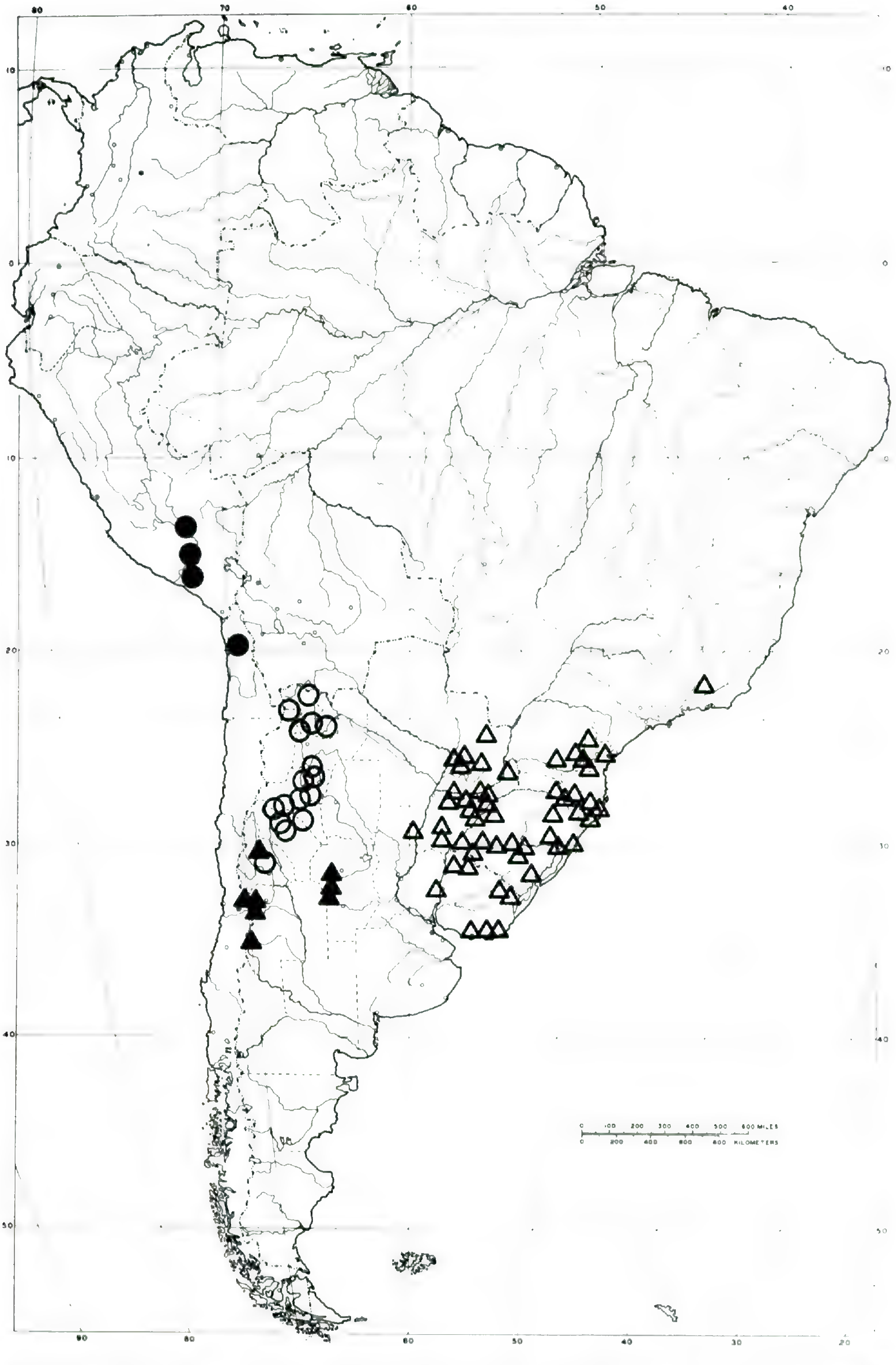


FIGURE 225. Ranges of *Oenothera peruana* (dots), *O. lasiocarpa* (circles), *O. santarii* (filled triangles), and *O. ravenii* subsp. *ravenii* (hollow triangles).

leaves plane or undulate at the margins, irregularly serrate, the teeth blunt. Inflorescence branched or unbranched. Floral tube 1.2–2.5 cm long. Buds oblong to lanceolate in outline, green to yellowish green, often red striped at the junction of the sepals with the floral tube, 0.6–1.2 cm long, 3–4 mm thick. Sepals often flecked with dark red; apices of the sepals erect, 1–2 mm long. Petals obovate to very broadly obovate, 0.7–1.5 cm long. Anthers 4–6 mm long. Filaments 5–10 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.8–3.2 cm long. Stigma lobes 3–4 mm long. Ovary 1.3–1.5 cm long. Capsule (2–)3–4.5 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.2–1.5 mm long, 0.6–0.8 cm wide. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Buenos Aires, dunes ca. 2 km SE of Argerich in the research terrain of the Universidad del Sur, 37 km W of Bahía Blanca, 9 Jan. 1968, *K. A. Santarius 455* (MO-2155721, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 236): Known only from the provinces of Buenos Aires, La Pampa, Neuquén, and Chubut, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Dunes ca. 2 km SE of Argerich in the research terrain of the Universidad del Sur, 37 km W of Bahía Blanca, *Santarius 455**, *457**, *460**, *465* (DUSS; 457 also CTES; *455*, *457* also M, MO). NEUQUÉN: Sandy places in the SE part of the city of Neuquén, *Santarius 542**, *558*, *560*, *569**, *575** (DUSS; *542*, *569* also CTES, M; *542*, *569*, *575* also MO). Sandy and waste places in the irrigation ditches of the farm "Granja LU" in the SE part of the city of Neuquén, *Santarius 567**, *590**, *594*, *595* (DUSS; *590* also CTES, M; *567*, *590* also MO). Stony places at Río Limay, 6 km E of Piedra del Águila, *Santarius 597**, *598**, *604** (DUSS; *598* also CTES, M; *598*, *604* also MO).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: Necochea, *Hicken 4662* (LIL). Laguna Brava near Gral. Pueyrredón, 100 m, *Descole in 1938* (LIL). San Clemente near Gral. Lavalle, *Cabrera 4262* (GH). Bahía Blanca, *Claraz in 1884* (G). Dunes near Bahía San Blas, *Fabris & Schwabe 5012* (LP). Pigué near Saavedra, *Burkart 4713* (MO). Sierra de Curamalal, *Cabrera 5433* (LP). Sierra La Tinta, El Sombrerito, 400 m, *Spegazzini 41* (BAB). Est. Sta. María at Río Colorado near Villarino, *Hunziker 4452* (POM, SI). Campo "La Susana" near Est. Peralta, 320 m, *Huidobro 1177* (LIL, NY, S, SI). Sierra de la Ventana, *Molfino 46137* (BAB); *Gomez 11785* (BAA, MO). LA PAMPA: Guatrache, *Williamson in 1925* (SI). NEUQUÉN: Bajada del Manzano, 20 km S of Zapala, *Ancibor 90245* (BAA). RÍO NEGRO: Choele Choel near Perellaneda, 152 m, *O'Donell 1795* (NY). Dep. Conesa, China Muerte near Laguna del Mate in the valley of Río Negro, 60 km E of Carmen de Patagones, *Krapovickas 2078* (RSA); *Hunziker 479* (CORD, RSA). CHUBUT: Valle de Las Plumas, *Gerling 137* (POM). Cabo Raso, *Müller 24* (CORD). Between Travesia de Rawson and the Cordilleras, *Illin 16* (SI).

It has not yet been possible to analyze the complexes involved in the origin of *O. bahia-blancae* with any degree of certainty. On the basis of the strigillose pubescence and the relatively small leaves, one might suggest that one of the complexes of *O. mendocinensis* is involved, while the other might be an altered complex derived from *O. longiflora* and with genes for smaller flowers than in that species. Such a complex, ultimately derived from *O. longiflora*, is represented both in *O. parodiana* of series *Allochroa* and in *O. cordobensis* of series *Clelandia.*

25. **Oenothera picensis** Philippi, Anales Mus. Nac. Chile, Bot. 1891: 22. 1891. Figs. 65–66, 140–142, 222.

Annual herb with an erect or somewhat decumbent main stem, not forming a rosette, simple or branched near the base, 2–10 dm tall. Plants very densely to sparsely long-villous, the hairs soft, densely to sparsely short-villous and glandular-pubescent. Cauline leaves narrowly elliptic to lanceolate, acute, acute to truncate at the base, sessile, 3.5–10 cm long, 0.5–2 cm wide; bracts narrowly oblong or narrowly lanceolate to narrowly ovate, acute, truncate to subcordate at the base, sessile, 2.5–6 cm long, 0.5–2 cm wide, longer than the capsule they subtend or subequal to them, occasionally shorter; leaves plane or coarsely undulate at the margins, irregularly serrate, the teeth blunt. Inflorescence mostly branched. Floral tube 1.5–4.5 cm long. Buds oblong to lanceolate in outline, 0.7–1.7 cm long, 3–5 mm thick, often red striped at the junction of the sepals with the floral tube. Sepals often flecked with dark red; apices of the sepals 1–2 mm long, mostly erect. Petals broadly obovate to very broadly obovate, sometimes broadly elliptic, 0.7–2.5 cm long. Anthers 5–12 mm long. Filaments 5–15 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2–6 cm long. Stigma lobes 3–6 mm long. Ovary 1–2 cm long. Capsule (2–)2.5–4(–4.5) cm long, 3–4 mm thick. Seeds elliptic to broadly elliptic in outline, 1.2–2 mm long, 0.5–0.8 mm thick, brown. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14, ring of 10 and ring of 4 or ring of 8 and ring of 6 at meiotic metaphase I).

Lectotype: Chile, Prov. Atacama, oasis of Pica, Mar. 1885, *R. A. Philippi* (SGO-52850, GH photograph).

Distribution (Fig. 237): At the foot of the Andes in Argentina in the provinces of Jujuy, Salta, Tucumán, Catamarca, San Juan and Mendoza, and also in the provinces of Buenos Aires, Córdoba, San Luis, and Río Negro; on the western side of the Andes in Chile from the province of Antofagasta to Colchagua. *Oenothera picensis* subsp. *picensis* is adventive on the Juan Fernández Islands and in the provinces of Bío-Bío and Malleco in southern Chile.

Each of the three subspecies of *O. picensis* is made up of chromosomal complexes originating from *O. odorata* on the one hand and *O. affinis* on the other. They must have originated independently from one another, however, judging from their completely distinct areas of distribution. One of the most important characteristics of *O. picensis* is that it forms no rosette, a characteristic that can be traced back to the influence of *O. affinis*, one of its parents. The soft pubescence is also reminiscent of *O. affinis*, whereas the width of the bracts at their base is a characteristic of *O. odorata*.

Key to the Subspecies

1. Plants densely long-villous.
    2. Floral tube 2–4.5 cm long .... 25a. subsp. *picensis*
    2′. Floral tube 1.5–2 cm long .... 25c. subsp. *bonariensis*

1′. Plants not densely long-villous.
    3. Petals 1.5–2.5 cm long .... 25a. subsp. *picensis*
    3′. Petals 0.7–1.3 cm long .... 25b. subsp. *cordobensis*

FIGURE 226. Ranges of *Oenothera versicolor* (circles), *O. rubida* (filled triangles), *O. mendocinensis* (hollow triangles), and *O. ravenii* subsp. *chilensis* (dots).

25a. **Oenothera picensis** subsp. **picensis**.—FIG. 140.

O. odorata sensu Gillies ex Hooker, Bot. Misc. 3: 310. 1833, pro parte.
O. mollissima sensu Gillies ex Hooker, Bot. Misc. 3: 310. 1833.
O. mollissima sensu Reiche, Anales Univ. Chile 98: 476. 1897.
O. mollissima sensu Munz, Amer. J. Bot. 22: 659. 1935, pro parte; Revista Univ. (Santiago) 22: 266. 1937, pro parte.
O. affinis sensu Munz, Revista Univ. (Santiago) 22: 267. 1937, pro parte.
O. odorata "Erlangen" Haustein, Z. Indukt. Abstammungs- Vererbungsl. 84: 418. 1952; Cleland, Jap. J. Genet. 43: 332. 1968.
O. mollissima "Uspallata" Tandon & Hecht, Cytologia 21(3): 252. 1956.

Plants 4–10 dm tall. Plants densely to sparsely long- and short-villous, sparsely glandular-pubescent. Cauline leaves narrowly lanceolate to lanceolate, acute, 6–10 cm long, 0.5–1.3 cm wide; bracts lanceolate to narrowly ovate, acute, truncate to subcordate at the base, 3.5–6 cm long, 0.8–1.5 cm wide. Floral tube 2–4.5 cm long. Buds oblong to lanceolate in outline, 1.2–1.7 cm long, 4–5 mm thick. Petals very broadly obovate, 1.5–2.5 cm long. Anthers 7–12 mm long. Filaments 11–15 mm long. Style 3–6 cm long. Stigma lobes 4–6 mm long. Ovary 1.2–2 cm long. Capsule 2.5–3.5 cm long. Seeds elliptic in outline, 1.3–2 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–May.

Distribution (Fig. 237): In Chile from the province of Antofagasta to Colchagua; adventive on the Juan Fernández Islands and in the southern Chilean provinces of Bío-Bío and Malleco; on the east side of the Andes in the provinces of Mendoza and San Juan in Argentina.

Specimens examined from cultivated plants:

CHILE. VALPARAÍSO: Concón to Salinas near the border to Prov. Aconcagua, *Hjertung & Rahn 553** (CTES, DUSS, M, MO). Concón, N of Viña del Mar, *Göpel in 1961* (DUSS, MO).

ARGENTINA. MENDOZA: Uspallata, *Hecht 1964-78** (CTES, DUSS, M, MO). Stony places at Río Mendoza near the bridge of Ruta 7, 10 km S of Uspallata, 1900 m, *Santarius 1549*, 1550** (DUSS; *1549* also CTES, M, MO). On rocks ca. 5 km S of Cacheuta, 23 km N of Luján de Cuyo, 1200 m, *Santarius 1551, 1553* (DUSS; *1553* also MO). Stony and waste places ca. 2 km N of Tupungato, 1250 m, *Santarius 1554*, 1556, 1564, 1565, 1570, 1571** (DUSS; *1554, 1564* also MO). At the road above El Peral, 6 km NW of Tupungato, 1350 m, *Santarius 1576** (DUSS, M, MO).

CULTIVATED: *O.* "*odorata*" from the Botanical Garden in Erlangen, Germany, received 1960* (CTES, DUSS, M, MO).

Additional specimens examined:

CHILE. ANTOFAGASTA: Chuquicamata, *Martin 173* (SI). Toconao, 2,300 m, *Ricardi 2998* (CONC); *Ivanovič 7713* (CONC). ATACAMA: La Pampa, valley of Río del Transito, 1,450 m, *Johnston 5861* (GH, K, POM). Est. Manflas, *Ricardi 3748* (CONC). La Higuerita near San Félix, 1,300 m, *Ricardi 3870* (CONC). Copiapó, *Ricardi 3625* (CONC); *Gigoux in 1885* (GH). Desert of Atacama, *Morong 1105* (F, MO, NY). COQUIMBO: Tulahuén, *Alamo 19175* (CONC). Punitaquí near Ovalle, *Jiles 1936* (CONC). ACONCAGUA: Portillo on road to Mendoza, *Diaz in 1861-62* (SGO). Río Blanco, 1,400 m, *Günther & Buchtien in 1928* (S). VALPARAÍSO: *Bueck in 1843* (HBG); *Wilkes* (NY); *Buchtien in 1895* (US). Olmué near Limache, *N.N. 1901* (HBG). Limache, *Behn 22798* (CONC). Reñaca valley, *Poulsen in 1951* (C). Between Concón and Salinas, *Hjerting & Rahn 553* (C). Viña del Mar to Concón, *Günther & Buchtien in 1928* (HBG). SANTIAGO: *Claude-Joseph 726* (US). Romeral at Río Yezo, *Biese 83* (GH, LIL). Chacayes at Río Yezo, *Biese 139* (LIL). Dunes near El Tabo, *Kohler 229* (CONC). San Antonio, *Looser 924* (SI). Dunes of Llolléo S of San Antonio, *Poulsen in 1952* (C). Valley of Maipo, between Obra and Canelo, *Looser 144-17* (SI). El Manzano near San José de Maipo, 870 m, *Montero in 1927* (GH, K); *Sparre in 1947* (S). Batuco, *Reiche* (SGO-061514); *Looser 2406* (POM), *257* (SI). COLCHAGUA: Talcaregoné,

Gay in 1831 (P). BÍO-BÍO: Trapatrapa (SGO-052829). MALLECO: Sta. Rosa, *Philippi in 1882* (SGO). *Islas Juan Fernández*: *Philippi in 1864* (SGO-052867); *Bertero 1486* (K, P). Masatierra, *Bürger* (GOET); *Skottsberg 141* (S, UPS); *Bock 22801* (CONC). Masafuera, Quebrada Casas, *Meyer 9352* (MO). Province unknown: Aeuleo, *Bertero 446* (W), *464*, *1185* (G, MPU, NY, P). Cerro S. Cristóbal, *N.N. in 1868* (W).

ARGENTINA. MENDOZA: *Jörgensen 131* (C). Mendoza, 800 m, *King 112* (BM); *Sanzin 87* (SI); *Loos 2390* (CORD). San Carlos, *Roig 5178* (CORD); *Covas 3492* (SI). Dep. Tunuyán, Campo de los Andes, 1,800 m, *Paci 713*, *727* (LIL); Barkley *20Mz126* (LIL, NY, P, W). Arroyo La Remonta, 1,500 m, *Melis & Paci 777* (LIL, NY); *Cáceres 76* (LIL, NY). Dep. Las Heras, Quebrada del Toro, 2,000 m, *Calastremé 72032* (BAB). La Gloria, *Ruiz Leal 963* (Leal). Villavicencio, *Burkart et al. in 1942* (SI-14176). Tupungato, *Ruiz Leal 2784b*, *2784* (Leal, POM), *2775* (Leal, LP). Dep. Lújan, Cacheuta, *Ruiz Leal 8734* (Leal, LIL). Potrerillo, 1,500 m, *Semper 401* (LIL); 1,600 m, *Garcia 374* (LIL). Dep. San Rafael, Río Diamante, *Reales 1966* (LIL). Aguo del Sapo, 1,200 m, *Ruiz Leal 7378* (Leal, LIL). Río Atuel, 1,400 m, *Wilczek 410* (G). Between Yagualito and Las Peñas, *Kurtz 5412* (CORD). Cordillera of Mendoza, Cordón de Sta. Elena, *Figueroa 15736* (CORD). Cordilleras, *Jensen-Haarup in 1904* (C, LD, S).

Specimens from plants cultivated in gardens:

Leningrad, seeds from Chile sent by Cuming, *in 1833* (LE). Kew, *in 1880* (K; as *O. holosericea*).

Among the F_1 generation hybrids between *O. affinis* and *O. picensis* subsp. *picensis* there are two classes of plants, one closely similar to each parent. The same occurs in hybrids between *O. odorata* and *O. picensis* subsp. *picensis*. Consequently, the parentage of this particular subspecies seems to be clearly demonstrated.

Since there is no evidence that chromosomally homozygous entities of this series have ever occurred in Chile, it seems most probable that the *O. affinis* complex in *O. picensis* subsp. *picensis* was derived from the complex heterozygous *O. affinis* that does occur in Chile, and that the *O. odorata* complex was derived via *O. stricta*. It is also possible, of course, that *O. stricta* has derived its *odorata*-complex from *O. picensis*. This seems improbable, however, since the *ravenii*-complex of *O. stricta* in Chile is much more widespread than the *affinis*-complex of *O. picensis*, so that one might surmise that the *odorata-ravenii* combination originated earlier than the *odorata-affinis* combination.

From Chile *O. picensis* subsp. *picensis* seems to have migrated over the Uspallata Pass to Argentina, where it seems to form occasional secondary hybrids with the homozygous *O. odorata*, judging by the presence of plants with relatively large flowers in the Argentine portion of the range of *O. picensis* subsp. *picensis*.

25b. **Oenothera picensis** subsp. **cordobensis** Dietrich, subsp. nov.—FIGS. 65–66, 141, 222.

O. mollissima sensu Munz, Physis 11: 282. 1933, pro parte.
Oenothera parodiana sensu Munz, Physis 11: 283. 1933, pro parte; Amer. J. Bot. 22: 662. 1935, pro parte.

Plantae 2.5–9 dm altae, plerumque pilis longis villosis dispersis praeditae, etiam pilis brevibus villosis glandulosibusque praeditae. Folia caulina anguste elliptica vel lanceolata, 3.5–5 cm longa, 0.5–1 cm lata; bractea anguste oblonga ad oblongam vel anguste lanceolata at lanceolatam, 2.5–3.5 cm longa, 0.5–1 cm lata, quam capsulas subtentas breviora vel subaequalia. Tubus floralis 3–4.5 cm longus. Gemmae ambito oblongae vel lanceolatae, 0.7–1.2 cm longae, 3–4 mm crassae. Sepala fusco-rubro saepe punctata; apices sepalorum 1–2 mm longi.

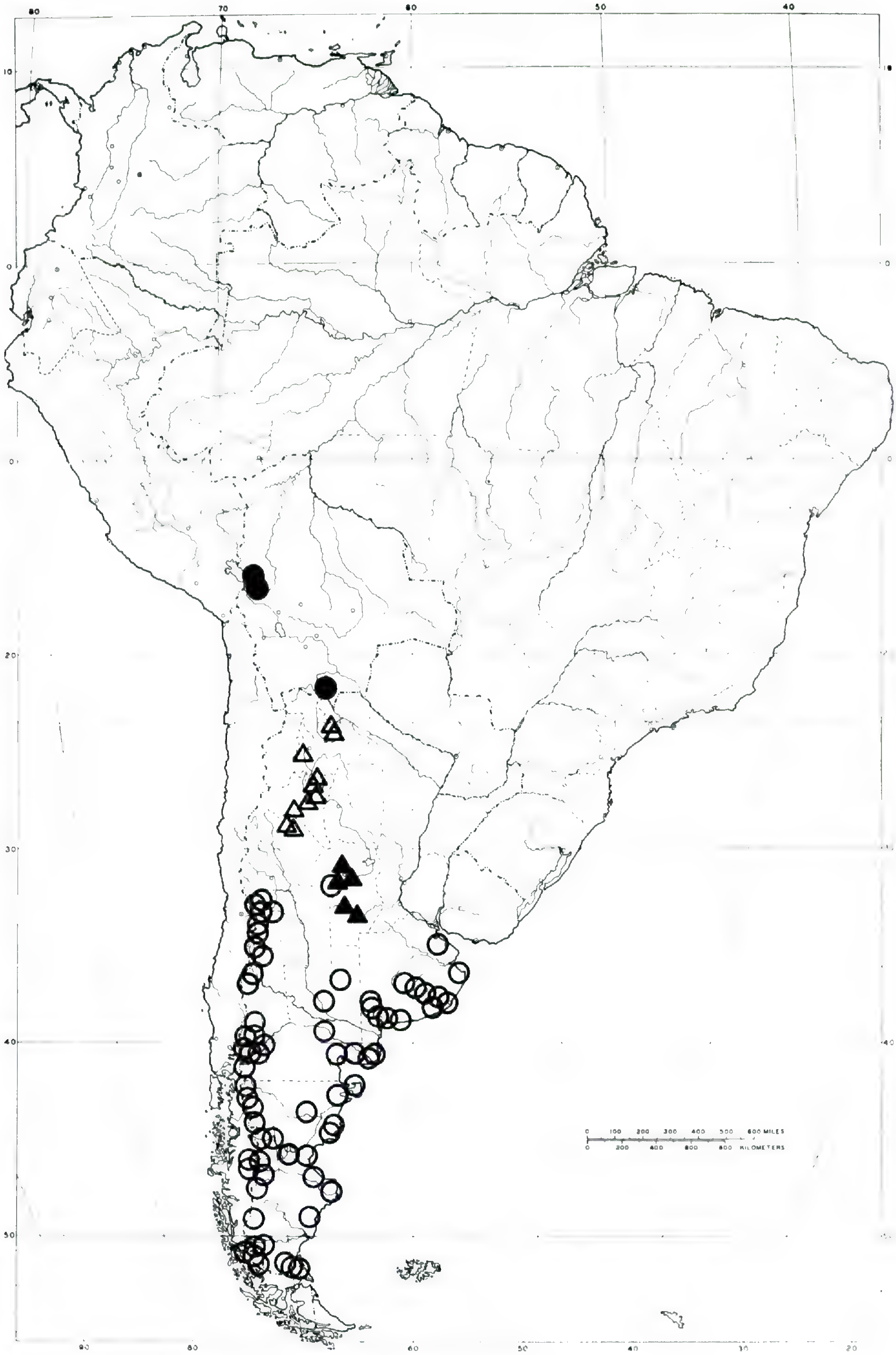


FIGURE 227. Ranges of *Oenothera longituba* (hollow triangles), *O. tarijensis* (dots), *O. odorata* (circles), and *O. cordobensis* (filled triangles).

Petala late elliptica vel late obovata ad latissime obovata, 0.7–1.3 cm longa. Ovarium 1.1–1.4 cm longum. Capsula (2–)3–4(–4.5) cm longa. Semina ambito late elliptica, 1.2–1.7 mm longa, 0.7–0.8 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 2.5–8 dm tall. Usually with scattered long-villous pubescence, but also densely short-villous and glandular-pubescent. Cauline leaves narrowly elliptic to lanceolate, 3.5–5 cm long, 0.5–1 cm wide; bracts narrowly oblong to oblong or narrowly lanceolate to lanceolate, 2.5–3.5 cm long, 0.5–1 cm wide, shorter than the capsules they subtend or subequal to them. Floral tube 3–4.5 cm long. Buds oblong to lanceolate in outline, 0.7–1.2 cm long, 3–4 mm thick. Sepals often flecked with dark red; apices of the sepals 1–2 mm long. Petals broadly elliptic or broadly obovate to very broadly obovate, 0.7–1.3 cm long. Anthers 5–7 mm long, ca. 1 mm wide. Filaments 5–10 mm long. Style 3.5–5 cm long. Stigma lobes 3–4 mm long. Ovary 1.1–1.4 cm long. Capsule (2–)3–4(–4.5) cm long. Seeds broadly elliptic in outline, 1.2–1.7 mm long, 0.6–0.8 mm thick. Self-pollinating and often cleistogamous. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 10 and ring of 4** at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Córdoba, Cuesta de San Roque near Córdoba, ca. 4 km of "Carlos Paz," 19 Dec. 1961, *G. Göpel* (MO-2155410, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 237): At low elevations, up to 1,300 m or rarely ascending to 1,800 m, in the provinces of Jujuy, Salta, Tucumán, Catamarca, Santiago del Estero, Córdoba, and San Luis, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. JUJUY: In the bed of Río Xibi Xibi SE of San Salvador de Jujuy, 1250 m, *Santarius 1805*, 1806*, 1807, 1809, 1812, 1815, 1816*, 1817, 1819, 1822, 1823, 1824, 1828, 1829, 1831–1833, 1835*, 1836, 1837, 1840* (DUSS; *1804, 1806, 1816, 1835* also CTES; *1805, 1806, 1816, 1835* also M; *1805, 1806, 1809, 1816, 1817, 1824, 1835* also MO). In the bed of Río Grande N of San Salvador de Jujuy, 1250 m, *Santarius 1845*, 1846**, 1847, 1848** (DUSS; *1848* also CTES, M; *1845, 1846, 1848* also MO). CÓRDOBA: Between Córdoba and Cuesta Blanca, *Göpel in 1961** (DUSS, M, MO). Villa Independencia near Córdoba, *Göpel in 1961** (CTES, DUSS, M, MO). Cuesta de San Roque near Córdoba, *Göpel in 1961** (CTES, DUSS, M, MO). Copina near Córdoba, *Göpel in 1961** (DUSS, M, MO).

Representative specimens examined:

ARGENTINA. JUJUY: *O'Donell 2802* (LIL, NY); *Kuntze in 1892* (NY). León, 1,700 m, *Cabrera et al. 13907* (BAB, LP). Shore of Río Xibi Xibi near San Salvador de Jujuy, 1,260 m, *Arnow 3642* (MO). SALTA: Río Pescado near Orán, *Alberti 71517* (BAB). Campo Quijano near Rosario de Lerma, *Meyer 3586* (F, GH, LIL, NY). Río Vaquero near Caldera, 1,200 m, *Sparre 1231* (S). Lesser near Calitera, 1,950 m, *Filipovicz 440* (LIL). El Ladil near Candelaria, *Montenegro 351* (LIL). Río Concha near Metán, *Herrera 28* (LIL). Quebradas of Río Toro and Río Blanco, *Vattuone 49, 134* (LIL, SI). TUCUMÁN: Arroyo Itaembé, *Meyer 11484* (LIL). El Timbo near Burroyacu, 600 m, *Venturi 2231* (US). Río Salí near Tucumán, 450 m, *Venturi 898a* (NY). CATAMARCA: *Castillón 1666* (SI). El Chorro near Ancasti, *Rojas Paz 16* (GH, LIL). Sierra de Ancasti, Ruta 66, *Hunziker & Di Fulvio 17097* (CORD). La Banda, *Spegazzini 29285* (BAB). El Portezuelo, *Bartlett 19613* (MICH, US). Dep. Pomán, Sierra de Ambato, between El Rincón and Las Casitas to Cerro Manchado, 2,300–2,500 m, *Hunziker & Arizo 20372* (CORD). Tinogasta, *Ahumada 56* (LIL). Yacutula, *Schickendantz 161* (CORD). El Alto, *Argañaraz 652, 674* (LIL). SANTIAGO DEL ESTERO: Ojo de Agua, *Balegno 152, 183, 1306* (LIL); *Garcia 893* (LIL). CÓRDOBA: Córdoba city, *Stuckert 22108* (CORD, MO). Santa María, 600 m, *Gutierrez 247* (LIL). El Durazno, 1,200 m, *Meyer & Sleumer 15702*

(LIL). Capilla del Monte, *Lanfranchi 633* (SI); *Hossens 210, 400, 427, 694* (CORD). Copina, 1,400 m, *Hieronymus 334* (P), *655* (CORD, GOET). Lago San Roque near Carlos Paz, *Bridarolli 265* (LP). Valle Hermoso, *Huidobro 138* (LIL). Las Rosas near La Falda, *Stuckert 16940, 18925* (G); *Wall in 1946* (S); *Job 506* (NY). Tanti, *Nicora 2923* (SI). Casa Bamba, *Krapovickas 1882* (LIL). Alta Gracia, 1,800 m, *Pierotti in 1944* (LIL, NY, S, US). Las Peñas near Totoral, *Balegno 1169* (LIL). Villa García, *Meyer in 1940* (F). Taninga, *Boelcke 7745* (BAA, MO). Mina Clavero, *Meyer 13386* (LIL). Cruz del Eje, 470 m, *Meyer 13043* (LIL). Unquillo, *Bruch in 1926* (F, NY). Cerro Saúce Punco near Tulumba, 700 m, *Meyer 13100* (LIL). Ascochinga, *Calderon 658* (BAA). Pampa de Achala, 2,200 m, *Hunziker 1402, 1403* (CORD). Cerro de Chaján near Río Cuarto, 500 m, *Hunziker 16504* (CORD). Sierra de Achiras, 800 m, *King 525* (BM). Sierra Chica, La Redución, *Burkart 7327* (SI). Rosario, *Bartlett 20165* (GH, MICH, US). Dean Funes near Ischilin, *Cuezzo 705* (BM, F, LIL, S). Dep. Río Segundo, Manfredi, *Krapovickas 6616* (BAB, CORD, LIL). Cosquín, 730 m, *Rodrigo 275* (NY, US). Villa de María at Río Seco, *Balegno 1458* (LIL). Gral. Paz, *Stuckert 3739* (CORD, G). Salsipuedes near Colón, *Dawson 84* (LP, NY); *Hunziker 1474* (CORD, LIL, RSA). Santa Catalina near Colón, *Dawson 436* (POM). Jesús María near Colón, *Balegno 1487* (LIL). Dep. Calamuchita, Arroyo Calmayo near Soconciro, *Bodenbender in 1925* (CORD). Champaquí, *Reutzell in 1944* (SI). SAN LUIS: Cerro El Morro, Est. La Morena, 1,100–1,400 m, *Hunziker 12589* (CORD, MO). Piedra Blanca near Merlo, 1,000 m, *Grassi 2090* (LIL). Sierra de Comechingones, El Rincón, *Hunziker 11754* (CORD). Encrucijada, *in 1879* (BM). Peñón Colorado, *Castellanos 29-380* (BA, POM). Valley of Río Quines, *Galander in 1882* (CORD). Est. Grande, *Vignati 7* (SI), *587* (LP). Dep. Capital, Portrero de los Funes, banks of Arroyo de los Molles, 980 m, *Lee Anderson 1963* (CORD). Nogoli, *Gez 76* (SI).

Oenothera picensis subsp. *cordobensis* can be distinguished from subsp. *picensis* especially through its smaller flowers, less dense long villous pubescence, and mostly oblong leaves. Evolution in the *affinis*-complex in this entity seems to have proceeded farther in the direction of small flowers than in subsp. *picensis*, judged from the fact that F_1 hybrids between subsp. *cordobensis* and homozygous *O. affinis* consist of two classes of plants, one resembling *O. picensis* with medium-sized flowers, and one a very small-flowered type of plant resembling *O. affinis*.

Introgression of genes from *O. ravenii* or *O. longiflora* is seen in the plants of *O. picensis* subsp. *cordobensis* which have red-flecked sepals or short bracts. This has probably come about by means of occasional hybridization between *O. picensis* and *O. parodiana* which grow with *O. picensis* subsp. *cordobensis* in the province of Córdoba. Evidently, the genes associated with the red flecking of the sepals are in the portion of the chromosomes in which crossing over occurs, for they seem to be transferred readily from one complex to another. *Oenothera ravenii* is the only chromosomally homozygous species in South America which displays this characteristic.

In *O. picensis* subsp. *cordobensis*, the flowers often fail to open at all and are therefore completely cleistogamous. Even though the sepals split apart, they remain attached by their apices, and the petals cannot unfold. In a sense, one could regard this as the ultimate reduction associated with complex heterozygosity, since self-pollination renders the opening of the flowers superfluous.

25c. **Oenothera picensis** subsp. **bonariensis** Dietrich, subsp. nov.—FIG. 142.

O. mollissima sensu Munz, Amer. J. Bot. 22: 659. 1935, pro parte.

Plantae 4–10 dm altae, densissime pilis longis, dense pilis brevibus, denseque pilis glandulosis praeditae. Folia caulina anguste lanceolata vel lanceolata, basi truncata vel subcordata,

FIGURE 228. Ranges of *Oenothera tafiensis* subsp. *tafiensis* (circles), *O. recurva* (dots), and *O. ravenii* subsp. *argentinae* (filled triangles).

4–10 cm longa, 1.3–2 cm lata; bractea lanceolata vel anguste ovata, 3.5–6 cm longa, 1.3–2.5 cm lata, basi truncata vel subcordata. Tubus floralis 1.5–2 cm longus. Gemmae ambito oblonga vel late oblonga, 0.7–1.2 cm longa, 4–5 mm crassa. Sepala non rubro-punctata; apices sepalorum 1.5–2 mm longi. Petala late obovata vel latissime obovata, interdum late elliptica, 1–1.7 cm longa. Ovarium 1.2–1.5 cm longum. Capsula 2.5–3.5 cm longa, 3–4 mm crassa. Semina ambito elliptica, 1.2–1.8 mm longa, 0.6–0.8 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 4–10 dm tall. Plants very densely long-villous, densely short-villous and glandular-pubescent. Cauline leaves narrowly lanceolate to lanceolate, truncate to subcordate at the base, 4–10 cm long, 1.3–2 cm wide; bracts lanceolate to narrowly ovate, 3.5–6 cm long, 1.3–2.5 cm wide, truncate to subcordate at the base. Floral tube 1.5–2 cm long. Buds oblong to broadly oblong in outline, 0.7–1.2 cm long, 4–5 mm wide. Sepals not red flecked; apices of the sepals 1.5–2 mm long. Petals broadly obovate to very broadly obovate, sometimes broadly elliptic, 1–1.7 cm long. Anthers 5–8 mm long. Filaments 6–10 mm long. Style 2.0–2.7 cm long. Stigma lobes 3–4 mm long. Ovary 1.2–1.5 cm long. Capsule 2.5–3.5 cm long, 3–4 mm thick. Seeds elliptic in outline, 1.2–1.8 mm long, 0.6–0.8 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 8 and ring of 6** at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 11 Aug. 1972. Source: Argentina, Prov. Buenos Aires, N end of the Sierra La Peregrina, S of km 25.5 of Ruta 226 between Mar del Plata and Balcarce, 7 Jan. 1968, *K. A. Santarius 370* (MO-2155204, holotype; CTES, DUSS, isotypes).

Distribution (Fig. 237): Provinces of Buenos Aires and Río Negro, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: N end of the Sierra La Peregrina, S of km 25.5 of Ruta 226 between Mar del Plata and Balcarce, *Santarius 370**, *374*, *389**, *393*, *395*, *397** (DUSS; 383, 397 also CTES; *370*, *389*, *397* also M, MO). Sierra de la Ventana, rocks and stony hills at both sides of the railroad, 1 km NE of La Pileta, 350 m, *Santarius 490**, *500*, *503*, *506*, *508*, *515** (DUSS; *490* also CTES, M; *490*, *500*, *515* also MO). RÍO NEGRO: Stony place at the ferry across the Río Limay at Ruta 237, 75 km SSW of Piedra del Águila, *Santarius 640*** (CTES, DUSS, M, MO).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: Sierra de la Ventana, 300 m, *Huidobro 1320* (BM, LIL, S). Valle de las Vertientes, *Huidobro 1442* (LIL, NY, S, SI). Tornquist, *Visetti 54318* (BAB). Sierra Ventana, *Molfino 31-1632* (POM). Arroyo Sauce Grande, *Bartlett 20032* (GH, MICH, SI, UC). Tornquist, 400 m, *Hunziker 584*, *515* (CORD); *Meyer 14264* (LIL); *Krapovickas 2112* (LIL, RSA); *Rossi & Bachmann 459* (LIL). Cerrito La Ruina NE of Tornquist, *Rossi 466* (LIL). Port of Bahía Blanca, *Hicken in 1899* (POM). Canteras near Tandil, *Huidobro 1721* (LIL, S). Tandil, *Parodi 1682*, *1799* (BAA). Sierras del Tandil, Parque Independencia, *Abbiatti 4207* (LP). Sierra Buenavista near Balcarce, *Hunziker 2309* (POM, SI). Sierra La Vigilancia near Balcarce, *Cabrera 17155* (LP). Cerro "La Peregrina" near Balcarce, *Grondona & Dawson 6339* (BAA); *Eyerdam et al. 23644* pro parte (GH). Mar del Plata, *Valentini 446* (SI). Coastal dunes of Pinamar near Gral. Madariaga, *Boelcke 9040* (BAA, MO). Dunes near Bahía San Blas, *Fabris 5012* (M). Mar Chiquita, *Pelosi 120* (LIL, SI).

Oenothera picensis subsp. *bonariensis* differs strikingly from the other two subspecies in its dense long villous pubescence. The *odorata*-complex of this subspecies is derived from the densely pubescent form of the species that occurs in the province of Buenos Aires. The *affinis*-complex very probably has come by way of *O. mollissima*, but the relatively small buds that are more or less oblong

FIGURE 229. Ranges of *Oenothera tafiensis* subsp. *parviflora* (filled triangle), *O. sandiana* (circles), *O. longiflora* subsp. *grandiflora* (hollow triangles), and *O. catharinensis* (dots).

in outline and the short floral tube suggests introgression from *O. indecora* subsp. *bonariensis.*

26. **Oenothera montevidensis** Dietrich, sp. nov.—FIG. 143.

Herba annua, non rosulata, plerumque caule principale oblique vel subdecumbente simplice vel circum basin ramoso 3–5 dm longo. Plantae dense vel sparse pilis longis villosis, densissime pilis brevibus villosus et glandulosis praeditae. Folia caulina cultrata vel lanceolata, acuta, basi acuta vel rotundata, sessilia, 2–4 cm longa, 0.5–1 cm lata; bractea lanceolata vel anguste ovata, acuta, basi truncata, sessilia, quam capsula subtenta breviora vel ad eas subaequalia, 2–2.5 cm longa, 0.5–1 cm lata; folia plana vel ad margines exigue undulata, irregulariter obtuseque serrata. Inflorescentia ramosa. Tubus floralis 1–1.5 cm longus. Gemmae ambito oblongae, 0.5–0.7 cm longae, 3–3.5 mm crassae, flavo-virentes; apices sepalorum 0.5–1 mm longi. Petala latissime obovata, 0.5–0.8 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 0.6–1.6 cm longum. Capsula 2–2.5 cm longa, 2–2.5 mm crassa. Semina ambito elliptica, 1.5–1.6 cm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Annual herb, not forming a rosette, mostly with an obliquely ascending or somewhat decumbent main stem, which is unbranched or branched near the base and 3–5 dm long. Plants densely to sparsely long-villous, also very densely short-villous and glandular-pubescent. Cauline leaves cultrate to lanceolate, acute, acute to rounded at the base, sessile, 2–4 cm long, 0.5–1 cm wide; bracts lanceolate to narrowly ovate, acute, truncate at the base, sessile, shorter than the capsules they subtend or subequal to them, 2–2.5 cm long, 0.5–1 cm wide; leaves plane or weakly undulate, irregularly serrate, the teeth blunt. Inflorescence branched. Floral tube 1–1.5 cm long. Buds oblong in outline, 0.5–0.7 cm long, 3–3.5 mm thick, yellowish green; apices of the sepals 0.5–1 mm long. Petals very broadly obovate, 0.5–0.8 cm long. Anthers 3–5 mm long. Filaments 5–7 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.5–2.2 cm long. Stigma lobes ca. 3 mm long. Ovary 0.6–1.6 cm long. Capsule 2–2.5 cm long, 2–2.5 mm thick. Seeds elliptic in outline, 1.5–1.6 mm long, 0.5–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 8 Aug. 1972. Source: Uruguay, Dep. Montevideo, dunes near Carrasco and Miramar, 26 Dec. 1967, *K. A. Santarius 1* (MO-2155207, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 235): Found only in the departments of Canelones and Montevideo in Uruguay.

Specimens examined from cultivated plants:

URUGUAY. MONTEVIDEO: Dunes near Carrasco and Miramar, *Santarius 1*, 9, 11, 12, 15*, 17, 18, 27, 28* (DUSS; *1* also M; *1, 9* also MO).

Additional specimens examined:

URUGUAY: MONTEVIDEO: Carrasco, *Rosengurtt 850* (POM); *Courbon in 1856* (P); *Olazarri 205* (LIL). CANELONES: Bank of Arroyo Carrasco, *Rosengurtt B430* (LP, POM).

Superficially, *O. montevidensis* would seem to be a derivative of *O. mollissima,* but it is also very similar to *O. indecora* subsp. *indecora.* It can be distinguished from the latter by its thicker capsules, larger seeds, usually denser pu-

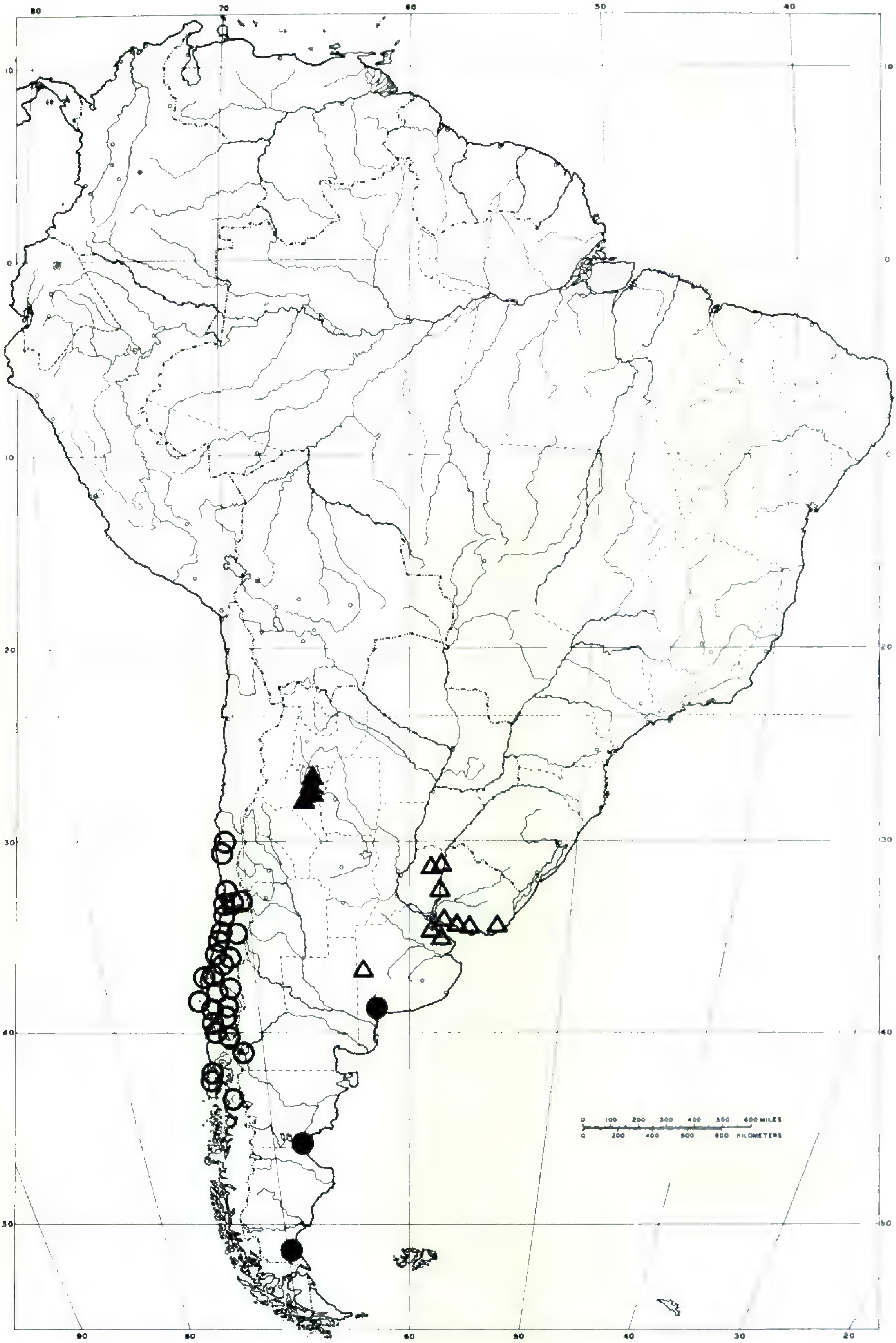


FIGURE 230. Ranges of *Oenothera pedunculifolia* (filled triangles), *O. longiflora* subsp. *longiflora* (hollow triangles), *O. rivadaviae* (dots), and *O. stricta* subsp. *stricta* (circles).

bescence, unflecked sepals, and absence of a rosette. Results from experimental hybridization suggest that one of the genomes of *O. montevidensis* has been derived from *O. indecora* subsp. *indecora*, while the other is an *affinis*-complex derived from *O. mollissima*. All F_1 hybrids between *O. montevidensis* and the chromosomally homozygous *O. indecora* subsp. *indecora* have resembled *O. montevidensis*, but others which were in effect reconstituted *O. indecora* could probably be obtained with further crossing. Similarly, F_1 hybrids with *O. mollissima* all resembled *O. montevidensis*.

27. **Oenothera pseudolongiflora** Dietrich, sp. nov.—FIG. 144.

Herba annua vel biennis, erecta, rosulata, caulis principalis ramosis ramisque arcuate e rosula ascendentibus, 8–15 dm alta. Plantae strigulosae, praecipue ad basin, etiam dense ad sparse pilis longis brevibusque villosis sparseque eis glandulosis praeditae. Folia rosulae anguste oblonga vel angustissime elliptica, acuta, sessilia vel lamina in petiolum gradatim decrescens, 15–20 cm longa, 1.5–2 cm lata; folia caulina anguste oblonga vel angustissime elliptica, acuta, basi acuta vel rotundata, sessilia, 5–10 cm longa, 1–1.8 cm lata; bractea anguste lanceolata vel lanceolata, acuta basi truncata vel subcordata, sessilia, 2–2.5 cm longa, 0.7–1 cm lata, quam capsula subtenta breviora; folia plana, remote obtuseque vel acute serrulata. Inflorescentia ramosa. Tubus floralis 4–6.5 cm longus. Gemmae ambito anguste oblongae vel oblongae, 1.1–1.7 cm longae, 3.5–7 mm crassae, plerumque junctura sepalorum tubo florali rubrofasciatae. Sepala flavo-virescentia; apices sepalorum ca. 1.5 mm longi, erecti. Petala latissime obovata, interdum basi indistincte rubro-maculata, 1.5–2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.5–2 cm longum. Capsula 3–4 cm longa, 3–4 mm crassa. Semina ambito elliptica, 1.1–1.3 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual or biennial herb, forming a rosette, with a branched main stem and side branches arching upward from the rosette, 8–15 dm tall. Plants strigillose, especially near the base, and also densely to sparsely long- and short-villous and sparsely glandular-pubescent. Rosette leaves narrowly oblong to very narrowly elliptic, acute, sessile or gradually narrowed to the petiole, 15–20 cm long, 1.5–2 cm wide; cauline leaves narrowly oblong to very narrowly elliptic, acute, acute to rounded at the base, sessile, 5–10 cm long, 1–1.8 cm wide; bracts narrowly lanceolate to lanceolate, acute, truncate to subcordate at the base, sessile, 2–2.5 cm long, 0.7–1 cm wide, shorter than the capsules they subtend; leaves plane at the margins, remotely serrate, the teeth blunt or sharp. Inflorescence branched. Floral tube 4–6.5 cm long. Buds narrowly oblong to oblong in outline, 1.1–1.7 cm long, 3.5–7 mm thick, usually red striped at the junction of the sepals with the floral tube. Sepals yellowish green; apices of the sepals ca. 1.5 mm long, erect. Petals very broadly obovate, sometimes with an indistinct red spot at the base of each one, 1.5–2 cm long. Anthers 8–10 mm long. Filaments 10–12 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 5–7.5 cm long. Stigma lobes 5–6.5 mm long. Ovary 1.5–2 cm long. Capsule 3–4 cm long, 3–4 mm thick. Seeds elliptic in outline, 1.1–1.3 mm long, 0.5–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–May.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 14 Aug. 1972. Source: Argentina, Prov. Buenos Aires, sandy soil

FIGURE 231. Ranges of *Oenothera scabra* (hollow triangles), *O. indecora* subsp. *indecora* (circles), *O. stricta* subsp. *altissima* (filled triangles), and *O. arequipensis* (dots).

at a road on Isla Santiago near La Plata, 5 Jan. 1968, *K. A. Santarius 269* (MO-2155209, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 235): Known only from the region of La Plata, province of Buenos Aires, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Punta Lara near La Plata, *Göpel in 1961** (CTES, DUSS, M, MO). Sandy soil at a road on Isla Santiago near La Plata, *Santarius 269*, 270, 272, 274* (DUSS; *269* also M, MO).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: Punta Lara near La Plata, *Rodríguez 520* (LIL); *Rossi 25* (LIL). Isla Paulino, *Cabrera 7384* (GH, LP).

I have named this species *O. pseudolongiflora* because the herbarium specimens I have seen have been determined as *O. longiflora*. The similarity between these two species, however, involves only a general resemblance in habit. As shown by experimental hybridization, *O. pseudolongiflora* has one complex from *O. ravenii*, the second from *O. affinis*. The respective F_1 progenies consisted of two classes of plants, one resembling *O. pseudolongiflora*, the other the second parent. It is interesting that the rosette-forming habit of *O. ravenii* is expressed in *O. pseudolongiflora*, because in the other combinations involving *O. affinis*—*O. picensis*, *O. elongata*, and *O. acuticarpa*—no rosette is formed, just as in *O. affinis*.

In comparison with *O. ravenii*, *O. pseudolongiflora* has smaller flowers and, on the average, a longer floral tube—characteristics that are derived from *O. affinis*. *Oenothera pseudolongiflora* can be distinguished from the two chromosomally heterozygous subspecies of *O. ravenii* by its longer bracts and floral tube. It should not be confused with *O. longiflora* in view of its softer pubescence, in which the long hairs are only 20–30 mμ thick instead of 60–70 mμ as in *O. longiflora*.

Especially in view of its restricted distribution, it appears likely that *O. pseudolongiflora* may be a species of very recent origin.

28. **Oenothera parodiana** Munz, Physis 11: 283. 1933.—FIG. 76–82, 145–148, 223.

Erect or somewhat decumbent annual or biennial herb, forming a rosette, with a simple or branched main stem, the obliquely ascending or arching side branches arising from the rosette, 3–12 dm tall. Plants either exclusively densely strigillose or densely to sparsely strigillose, densely to sparsely long- and short-villous and glandular-pubescent, or densely to sparsely villous and glandular-pubescent. Rosette leaves narrowly oblong to narrowly elliptic or oblanceolate, acute, narrowly cuneate or acute to truncate at the base, sessile or short-petiolate, 10–20 cm long, 0.6–3 cm wide; cauline leaves narrowly oblong to lanceolate or oblanceolate, acute, rounded to truncate at the base, sessile, 2.5–15 cm long, 0.5–2.5 cm wide; bracts oblong to broadly oblong or lanceolate to ovate, acute to obtuse, truncate to subcordate at the base, sessile, 1–2 cm long, 0.5–1 cm wide, shorter than the capsules they subtend; leaves plane or ± evidently undulate at the margins, irregularly or regularly serrate, the teeth sharp or

blunt. Inflorescence usually branched. Floral tube 1–4.5 cm long, sometimes flecked and streaked with red. Buds oblong to broadly oblong or broadly elliptic to rotund in outline, green to yellowish green, often flushed with red, often red striped at the junction of the sepals with the floral tube, 0.5–1.5 cm long, 3–5 mm wide. Sepals often flecked with red; apices of the sepals 1–1.5 mm long, erect or divergent. Petals very broadly obovate, rounded or retuse, sometimes with a red basal spot on each one, 0.7–2.5 cm long. Anthers 3–9 mm long. Filaments 5–14 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.8–5 cm long. Stigma lobes 2.5–6 mm long. Ovary 1–2 cm long. Capsule 2–4 cm long, 2.5–5 mm thick, the valves often clearly separated at the end. Seeds elliptic in outline 1.1–1.7 mm long, 0.5–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I). Flowering time: October–May.

Type: Argentina, Prov. Buenos Aires, meadows of El Socorro, Pergamino, 8 Dec. 1926, *L. R. Parodi 7395* (GH, holotype; W, isotype).

Distribution (Figs. 236, 238–239): From the state of São Paulo to Rio Grande do Sul in Brazil; in Uruguay in the departments of Ártigas, Salto, Rivera, Paysandú, Soriano, Colonia, Tacuarembo, Durazno, Cerro Largo, Maldonado, Canelones, Montevideo, Florida, and Flores; in Argentina in the provinces of Misiones, Corrientes, Entre Ríos, Buenos Aires, Formosa, Chacó, Santa Fe, Córdoba, San Luis, La Pampa, Santiago del Estero, and Tucumán.

In an evolutionary sense, *O. parodiana* occupies a position similar to that of *O. sandiana* in series *Renneria*. One might claim, with a certain justification, that *O. parodiana* consists of all the remnants that have not been determined and classified in the series after all of the more clear-cut elements have been taken out. Confronted with the overwhelming diversity of small-flowered phenotypes of this affinity, the taxonomist must of necessity surrender, since the possibility of bringing a neat arrangement out of the group simply does not exist. No fewer than six complexes have participated in the origin of the array of forms here grouped as *O. parodiana*, derived respectively from *O. mendocinensis*, *O. odorata*, *O. ravenii*, *O. longiflora*, *O. indecora*, and *O. affinis*. Except for the local *O. catharinensis* of southern Brazil, these are all of the distinct complexes found in the series *Allochroa*.

From this whole variable array, I have been able to separate only two taxonomically useful entities, *O. parodiana* subsp. *strigulosa* and *O. parodiana* subsp. *brasiliensis*. The first has only strigillose pubescence, and is restricted to the province of Buenos Aires. The second resembles the chromosomally homozygous *O. ravenii* rather closely, but it is small flowered and has longer bracts owing to the influence of *O. affinis* in its genetic constitution. It occurs predominantly in the northeastern and eastern portions of the range of *O. parodiana*.

All other forms have been grouped under *O. parodiana* subsp. *parodiana*. In addition to plants that resemble the type of the species, there are others which almost fall into the range of variation of *O. bahia-blancae*. Still others appear to be very small-flowered plants of *O. picensis* subsp. *cordobensis*. Plants which

resemble *O. indecora* closely are not infrequent. Intermediates between the forms that most closely resemble these species and *O. ravenii* frustrate any effort to bring a logical subdivision into play.

There are no internal barriers to interspecific hybridization between the members of series *Allochroa*, and six of the seven available complexes appear to have been recombined in various ways in response to selective pressures to give rise to the array of small-flowered chromosomal heterozygotes grouped under *O. parodiana*. The evolution of self-pollination in these heterozygotes was probably facilitated by its prior existence in the homozygous species *O. mendocinensis* and *O. indecora*. All six of the complexes involved in the assembly of *O. parodiana* are represented together over a broad area in the eastern part of the range of series *Allochroa*.

In addition to uniform populations, there are others which display a great variability. Here and there segregating characteristics such as red flecking on the buds or a red basal spot on the petals crop up and suggest the sort of intermixing which is actively going on at the population level. Since the formation of a ring of 14 is constant in these populations, it can be assumed that a balanced system has evolved within the species whereby combinations of end arrangements leading consistently to this result are continually reformed.

Only a very detailed genetic analysis would lead to a more profound insight into the history of this complex. Such an analysis, if it were carried out, might lead to the taxonomic subdivision of the many forms here grouped under *O. parodiana* subsp. *parodiana*, or even to the recognition of additional species within this group.

Key to the Subspecies

1. Pubescence entirely strigillose .... 28b. subsp. *strigulosa*
1′. Pubescence villous and glandular-pubescent, often also strigillose.
    2. Floral tube 1–2 cm long; petals 0.7–1.2 cm long .... 28a. subsp. *parodiana*
    2′. Floral tube 2.5–4.5 cm long; petals 1.5–2.5 cm long .... 28c. subsp. *brasiliensis*

28a. **Oenothera parodiana** subsp. **parodiana**.—Figs. 76–82, 145–146, 223.

O. argentinae H. Lév. & Thell. var. *heterotricha* Kloos & Thell., Ned. Kruidk. Arch. 1921: 100. 1921. Lectotype: Netherlands, Weert, oatfield near the Karelke meal factory, *A. W. Kloos in 1920* (BAS).

Plants erect or somewhat decumbent, 3–7 dm tall. Strigillose, villous and glandular-pubescent, or only villous and glandular-pubescent. Rosette leaves 7–12 cm long, 0.8–1.2 cm wide; cauline leaves 2.5–6 cm long, 0.6–1 cm wide; bracts 1–2 cm long, 0.5–0.8 cm wide; leaves plane or ± evidently undulate at the margins. Floral tube 1–2 cm long. Buds oblong to broadly oblong or elliptic to broadly elliptic, 5–8 mm long, 3–5 mm thick. Petals 0.7–0.2 cm long. Anthers 4–8 mm long. Filaments 6–11 mm long. Style 2–3.5 cm long. Stigma lobes 3–5 mm long. Capsule 2.5–3 cm long, 3.5–3.5 cm thick. Seeds 1.3–1.5 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I).

Distribution (Fig. 238): Found in the departments of Ártigas, Salto, Paysandú, Soriano, Rivera, Tacuarembo, Durazno, Flores, Florida, Canelones, Montevideo, Cerro Largo and Colonia in Uruguay, and in the provinces of Corrientes, Entre Ríos, Santa Fe, Buenos Aires, Córdoba, San Luis, La Pampa, Santiago del Estero, and Tucumán in Argentina.

Specimens examined from cultivated plants:

URUGUAY. COLONIA: Sandy places, port of Juan L. Lacaze, *Santarius 54*, 55*, 56–59, 60*, 61*, 62, 63*, 64, 65, 66** (DUSS; *55, 61, 63, 66* also CTES; *54, 55, 61, 63, 66* also M; *54, 55, 57, 61, 62, 63, 65, 66* also MO). FLORIDA: At the railroad 1 km NE to 3 km SW of Mansavillagra, *Santarius 207*, 210*, 211** (DUSS; *207* also CTES, M; *207, 211* also MO). 3 km S of Arrayán on Ruta 7, *Santarius 232*, 233, 235*, 236, 289–240, 241** (DUSS; *232, 235, 241* also CTES, M; *232, 236, 241* also MO). 5 km S, *Santarius 243*, 244–247, 248*, 249–253* (DUSS; *248* also CTES, M; *243, 248* also MO).

ARGENTINA. BUENOS AIRES: Stony, grazed hills 2 km W of La Pileta in the Sierra de la Ventana, 350–400 m, *Santarius 468*, 469*, 470*, 471, 472*, 474, 479*, 480, 483, 485*, 488, 489* (DUSS; *468, 469, 472, 479, 485* also CTES; *468, 469, 472, 474, 479, 485* also M; *468, 469, 472, 474, 479, 483, 485* also MO). Sierra de la Ventana, rocks and stony hills on both sides of the railroad, 1 km NE of La Pileta, 350 m, *Santarius 494* (CTES, DUSS, M, MO). Sandy places at the coast of Villa del Mar, 5 km NW of Punta Alta, *Santarius 516** (CTES, DUSS, M, MO). Dunes at the road from Villa del Mar to Ruta 229, 5 km NNE of Punta Alta, *Santarius 538*, 541* (DUSS; *538* also MO). TUCUMÁN: Stony places at Río Salí near the bridge of Ruta 9, E of Santa María de Tucumán, 420 m, *Santarius 1655*, 1656** (DUSS; *1655* also M). LA PAMPA: Near La Gloria, *Conrad & Dietrich 57** (DUSS).

Representative specimens examined:

URUGUAY. ÁRTIGAS: *Bartlett 21069* (F, GH, MICH, NY, UC, US). Between Río Uruguay and Arroyo Itacumbú, *Rosengurtt 10510* (MVFA). SALTO: *Felippone 3573* (G). Km 550 at Ruta 3, *Arrillaga 1707* (MVFA). PAYSANDÚ: Ártigas, *Arrillaga 1432* (MVFA). Km 475 at Ruta 3, *Puerto 11305* (MVFA). SORIANO: Est. Media Agua, *Izaguirre 294* (MVFA). Mercedes, *N.N. 181* (POM). COLONIA: Punta Gorda, *Rosengurtt 8639* (MVFA). Riachuelo, *N.N. 9* (BAA). Artilleras, Arroyo de Pintos near Puerto Platero, *Bartlett 20771* (US). RIVERA: Minas de Corrales, *Arrillaga 1221* (MVFA). TACUAREMBO: Valle Edén, *Arrillaga 1733* (MVFA). DURAZNO: Rincón del Bonete, *Arrillaga 1896* (MVFA). FLORES: Río Yi, *Rosengurtt B466* (POM). FLORIDA: Mansavillagra, *Rosengurtt B703* (POM). Arroyo Timote, *Rosengurtt B703* (SI). CANELONES: Arroyo del Saúce, W of Solís, *Bartlett 20968* (GH, MICH, US). Independencia, *Herter 162a* (LIL, SI). MONTEVIDEO: *Isabelle in 1838* (W); *Kuntze in 1892* (CORD); *Bartlett 20681* (MICH, US). Parque Lecoq, *Osorio 669* (LIL). CERRO LARGO: Between Río Negro and Aceguá, *Rosengurtt 851* (POM). Bañado Medina, *Rosengurtt B2518* (GH, LIL, P, POM). Arroyo Malo at Ruta 26, *Lema 7887* (MVFA).

ARGENTINA. CORRIENTES: Santo Tomé, *Pierotti 5571* (LIL). Tabay, *Krapovickas & Cristóbal 13752* (LP). At Ruta 14 near Mercedes, *Cano 1966* (BAB). Dep. Monte Casero, Libertad W of Curuzú, *Ibarrola 2514* (LIL, NY, S). Between Ruta 27 and Río Corrientes near Esquina, *Krapovickas et al. 27112* (CTES, MO). ENTRE RÍOS: Concepción del Uruguay, *Meyer 10437* (LIL). Colón, *Meyer 10565, 10646, 10705* (LIL). Concordia, *Burkart 23063* (MO, SI). Río Ceibo, *Burkart 5119* (MO). BUENOS AIRES: Est. Tropezón near 3 de Febrero, *Burkart 4564* (CTES, MO). Bahía San Blas, *Cabrera 4775* (GH, LP, SI). Monte Hermoso, *Carette in 1916* (NY). Casalins, *Fistolera 179* (POM). Libertad near Merlo, *Mazzucconi 669* (BAB). Salalé near Gral. Pintó, *Hicken 4857* (LIL, SI). Castelar, *Lourteig 279, 360* (LIL). Balcarce, Santa Amarante, *Crovetto 1575* (LIL). Trenque Lauquén, 100 m, *Hunziker 4000* (POM). Elizalde near La Plata, *Dawson 986* (LP). Tandil, *Troncoso in 1937* (K). Junín, *Schulz 5627* (LIL); *Clos 3890, 3950* (BAB). Tornquist, *Rossi & Bachmann 458* (LIL); *Erettowi 2780* (MO); *Kühnemann 224* (RSA). Pringles, *Osten 143* (BREM). Villa Udaondo, *Vervoorst 5527* (L). SANTA FE: San Cristóbal, *Balegno 591, 739* (LIL). Km 308 at Ruta 8, between Hughes and Sta. Emilia, *Cano 2784* (BAB). Aurelia near Santa Fe, *Feddersen in 1889* (C). Malabrigo, *Parodi 11222* (POM). Dep. Capital, between Recreo and Loma Río Salado, *Achenbach 421* (SI). CÓRDOBA: San Justo, *Balegno 915* (LIL). Sierra Grande, Cuesta de las Calvas, 1,800 m, *Hunziker 9682* (RSA). Salsipuedes near Colón, *Hunziker 1471* (CORD). Pacheco de Melo near Laboulaye, *Hunziker 12776* (CORD, RSA). Between Mina Clavero and Pampa de Achala, *Di Fulvio 194* (CORD). Road from Tancacha to Río

Tercero, *Scala in 1924* (NY). San Javier, *Castellanos 10731* (RSA). Campino el Cuadrado, *Wall in 1946* (S). Roque Saenz Peña between Laboulaye and Salguero, *Hunziker 12791* (CORD, MO, RSA). Achiras, 800 m, *King 220* (BAB). Huinca Renancó, *King 262a* (BM). Dep. Calamuchita, Athos Pampa, *Hunziker 7087* (UC). SAN LUIS: Cerro Blanco near San Martín, *Hunziker & Cocucci 14657* (CORD). Dique Luján near San Martín, 800 m, *Hunziker & Cocucci 14991* (CORD). LA PAMPA: Catrilo, *Fortuna 57* (LIL, NY, UC). La Gloria, *Fortuna 18* (GH, LIL, NY). Lonquimay, *Fortuna 31* (GH, LIL, NY). Gral. Pico, *Burkart 9913* (LIL, SI). TUCUMÁN: Sierra del Alto, Graneros, road from Catamarca to Tucumán, *Zetarayan 9054* (LIL). Las Cuchillas near Burroyacú, 1,100 m, *Lillo 5319* (LIL). SANTIAGO DEL ESTERO: Ojo de Agua, *Conrad & Dietrich 178* (DUSS).

Specimens from outside of South America:

SOUTH AFRICA. CAPE: Vlottenburg, *Greef in 1969* (K). Dronfield, ca. 9 mi N of Kimberley, ca. 1,300 m, *Leistner 2931* (M). ORANGE FREE STATE: Distr. Glen, *Mostert in 1952* (PRE). LESOTHO: Distr. Tebetebeng, 1957, *Jacot-Guillarmod 2927* (PRE). Distr. Roma, ca. 1,750 m, *Ruch 1586* (PRE). NATAL: Distr. Camperdown, Nagle Dam, ca. 400 m, 1957, *Wells 1146* (PRE). TRANSVAAL: Belfast, 1909, *Leendertz 9202* (PRE). Distr. Potschefstroom, 1948, *Louw 1740* (K, PRE). Distr. Zoutpansberg, farm Rustfontein ca. 9 mi E of Louis Trichardt, 1,300 m, 1955, *Schlieben 7309, 7319* (HBG, K, M). Distr. Pretoria, Queenswood Garden, *Meeuse in 1957* (PRE). Distr. Letaba, ca. 1,020 m, 1958, *Scheepers 270* (M). SOUTH WEST AFRICA: Distr. Windhoek, banks of the White Nossob near farm Bodenhausen, 1961, *Seydel 2686* (GOET, M, MO, SRGH).

RHODESIA. Distr. Lomagundi, Rothwell farm, 1970, *Marc 1087* (K, SRGH). Distr. Salisbury, 1970, *Linky 557* (SRGH). Distr. Melsetter, 1957, *Whellan 1443* (SRGH).

NETHERLANDS. W. Knollendam, near oil refinery "de Vrede," *Kloos in 1920* (L).

GERMANY. Emmerich, oil refinery, *Bonte in 1915* (BAS; as *O. argentinae* H. Lév. & Thell. var. *typica* Kloos & Thell. f. *corynocarpa* Thell.).

FRANCE. Dép. Nord, Dunkerque, *Bouly de Lesdain in 1925* (BAS).

Under this subspecies are grouped all small-flowered complex heterozygotes of series *Allochroa* with varying representation of *O. mendocinensis*, *O. odorata*, *O. ravenii*, *O. longiflora*, and *O. indecora* in their genetic make-up.

28b. **Oenothera parodiana** subsp. **strigulosa** Dietrich, subsp. nov.—FIG. 148.

O. parodiana sensu Munz, Physis 11: 283. 1933, pro parte; Amer. J. Bot. 22: 662. 1935, pro parte.

Plantae erectae, 3–7 dm altae, nonnisi strigulosae. Folia rosulae 7–12 cm longa, 0.6–1 cm lata; folia caulina 4–6 cm longa, 0.5–1 cm lata; bractea 0.9–2 cm longa, 0.5–1 cm lata; folia valde ad margines undulata. Tubus floralis 1.3–2.5 cm longus. Gemmae ambito oblongae vel anguste ovatae, 0.7–1.3 cm longae, 3–4 mm crassae. Petala 1–1.5 cm longa. Capsula 2–3.5 cm longa, 2.5–3.5 mm crassa. Semina 1.2–1.7 mm longa, 0.6–0.8 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants erect, 3–7 dm tall. Plants exclusively strigillose. Rosette leaves 7–12 cm long, 0.6–1 cm wide; cauline leaves 4–6 cm long, 0.5–1 cm wide; bracts 0.9–2 cm long, 0.5–1 cm wide; leaves evidently undulate at the margins. Floral tube 1.3–2.5 cm long. Buds oblong to narrowly ovate in outline, 0.7–1.3 cm long, 3–4 mm thick. Petals 1–1.5 cm long. Anthers 3–5 mm long. Filaments 5–8 mm long. Style 1.8–3 cm long. Stigma lobes 2.5–3 mm long. Capsule 2–3.5 cm long, 2.5–3.5 mm thick. Seeds 1.2–1.7 mm long, 0.6–0.8 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I).

Type: University of California Second Botanical Garden Expedition, 1938–1939, Argentina, Prov. Buenos Aires, 7 km E of Mar de la Plata, sandy soil, exposed high coastal bluffs, in reach of spray, full sun, 50 m, 10 Dec. 1938, *W. J. Eyerdam, A. A. Beetle & E. Grondona 23610* (UC, holotype; GH, K, NA, isotypes).

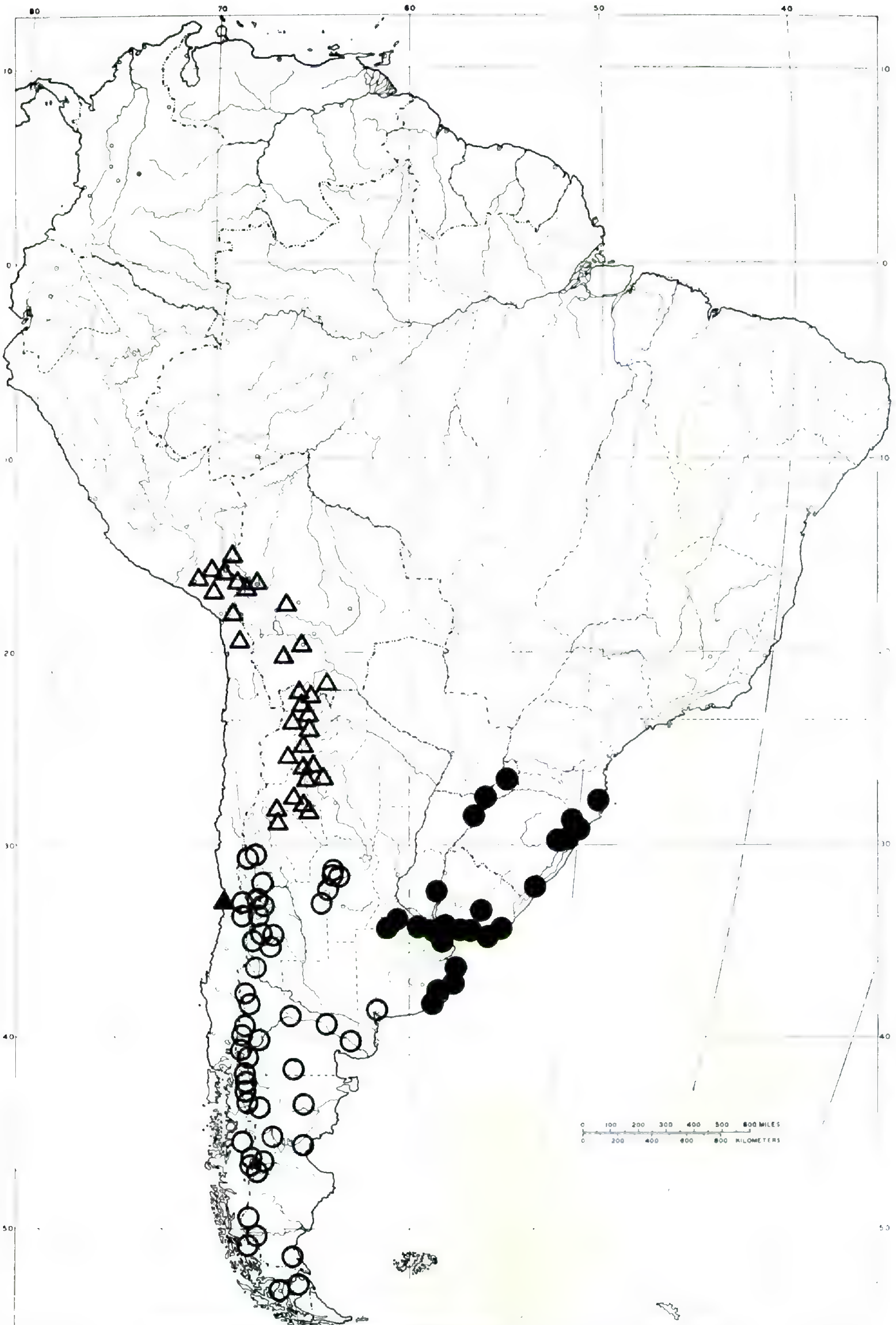


FIGURE 232. Ranges of *Oenothera nana* (hollow triangles), *O. mollissima* (dots), *O. grisea* (filled triangle), and *O. magellanica* (circles).

Distribution (Fig. 239): Only known from the province of Buenos Aires, Argentina.

Specimens examined from cultivated plants:

ARGENTINA. BUENOS AIRES: Sierra de la Ventana, at the road 2 km W of La Pileta, 300 m, *Santarius 466**, *467* (DUSS).

Additional specimens examined:

ARGENTINA. BUENOS AIRES: *Floyer in 1894* (K). Pergamino, *Parodi 8806* (POM); *Innes in 1914* (K). Bahía San Blas, *Fabris & Schwabe 5012* (LP, RSA). Ituzaingó, *Holmberg 119* (SI). Necochea, *Hicken in 1913* (SI). Trenque Lauquén, 100 m, *Hunziker 4017* (POM). Gral. Pinto, *Hicken 5* (POM). Pila, *León 1901* (BAA). Est. "La Argentina" near Lobería, *Grondona 12957* (BAA). Cerro Redondo near Olavarria, *Krapovickas 3370* (LIL). Sierra de las Tunas, Nuevo Cerro de la Cruz near Cnel. Suárez, *Rossi & Bachmann 464* (LIL). Bahía Blanca, *Soriano 456* (BAB, SI). Sierra La Vigilancia near Balcarce, *Fabris 2614* (CTES, LP). Balcarce, *Crovetto 2487* (BAB). La Copelina between Mar de la Plata and Balcarce, *Spegazzini 89* (BAB). Sierra de Curumalal, *Holmberg 2200* (CORD); *Parodi 10362* (BAA, POM); *Hicken 4* (POM); *Spegazzini 6861* (BAB, POM). Pigué, *Spegazzini 38, 77* (BAB); *Burkart 4713, 4794, 4795* (BAA); *Parodi 10405* (BAA). Est. San Carlos near La Pusana, *Huidobro 1282* (LIL). Cerro La Morediza near Tandil, *Huidobro 1747* (LIL). Gral. Pueyrredón, *Rodríguez 456* (LIL, NY). Punta Mogotes near Gral. Pueyrredón, *Rodríguez 436* (LIL). Sierra de los Padres near Gral. P., *Calderón 543* (MO). Dunes between Mar de la Plata and Miramar, *Hunziker 2202* (SI). Between Asito Unzuá and Parque Camet near Mar de la Plata, *Pelosi 64* (SI). Mar de la Plata, *Hicken 226* (SI), *227* (POM, SI). Sierra la Brava near M. de P., *Hicken 228* (SI). Mar de la Plata, *Valentini 36* (SI); *Bernard 42* (SI); *Carette in 1912* (SI); *Boffa 1* (LP). Gral. Alvaredo, *Crovetto 1498* (BAB, SI). Miramar, *Burkart 17834* (SI, US). Tandil, *Troncoso 1333* (F, LIL, SI); *Krapovickas 2942* (MO, RSA); *Clos 2233* (BAB). Sierra de la Ventana, *Fabris 2692* (LP); *Hicken 4666* (SI); *Boelcke 9587, 9588* (BAA). Est. Leines, *Alboff 125* (CORD). Cerro Naposta, 300 m, *Gómez 11701* (BAA). Tornquist, *Rossi & Bachmann 462, 463* (LIL); *Cabrera 4716* (P). La Pileta, *Cabrera 7340* (LP). Los Toldos near Gral. Viamonte, *Crovetto in 1967* (CTES).

Oenothera parodiana subsp. *strigulosa* resembles *O. bahia-blancae*, but is never villous. It has not yet been possible to carry out a program of experimental hybridization to analyze the genetic composition of this subspecies, but on the basis of its characteristics I suspect that *O. mendocinensis*, *O. odorata*, and *O. longiflora* may be involved.

28c. **Oenothera parodiana** subsp. **brasiliensis** Dietrich, subsp. nov.—FIG. 147.

O. parodiana sensu Munz, Physis 11: 283. 1933, pro parte.
Oenothera parodiana "Concordia" Cleland, Jap. J. Genet. 43: 332. 1968.

Plantae erectae, 7–12 dm altae, strigulosae, villosae, et glanduloso-pubescentes. Folia rosulae 8–20 cm longa, 1.2–3 cm lata; folia caulina 5–15 cm longa, 1–2.5 cm lata; bractea 1.5–2 cm longa, 0.7–1 cm lata; folia plana vel valde ad margines undulata. Tubus floralis 2.5–4.5 cm longus. Gemmae ambito anguste oblongae ad oblongas vel lanceolatae ad anguste ovatas, 1–1.5 cm longae, 4–5 mm crassae. Petala 1.5–2 cm longa. Capsula 3–4 cm longa, 3–4(–5) mm crassa. Semina 1.1–1.5 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Plants 7–12 dm tall, erect. Plants strigillose, villous, and glandular-pubescent. Rosette leaves 8–20 cm long, 1.2–3 cm wide; cauline leaves 5–15 cm long, 1–2.5 cm wide; bracts 1.5–2 cm long, 0.7–1 cm wide; leaves plane or evidently undulate at the margins. Floral tube 2.5–4.5 cm long. Buds narrowly oblong to oblong or lanceolate to narrowly ovate in outline, 1–1.5 cm long, 4–5 mm thick. Petals 1.5–2.5 cm long. Anthers 7–9 mm long. Filaments 9–14 mm long. Style 3.5–5 cm long. Stigma lobes 5–6 mm long. Capsule 3–4 cm long, 3–4(–5) mm

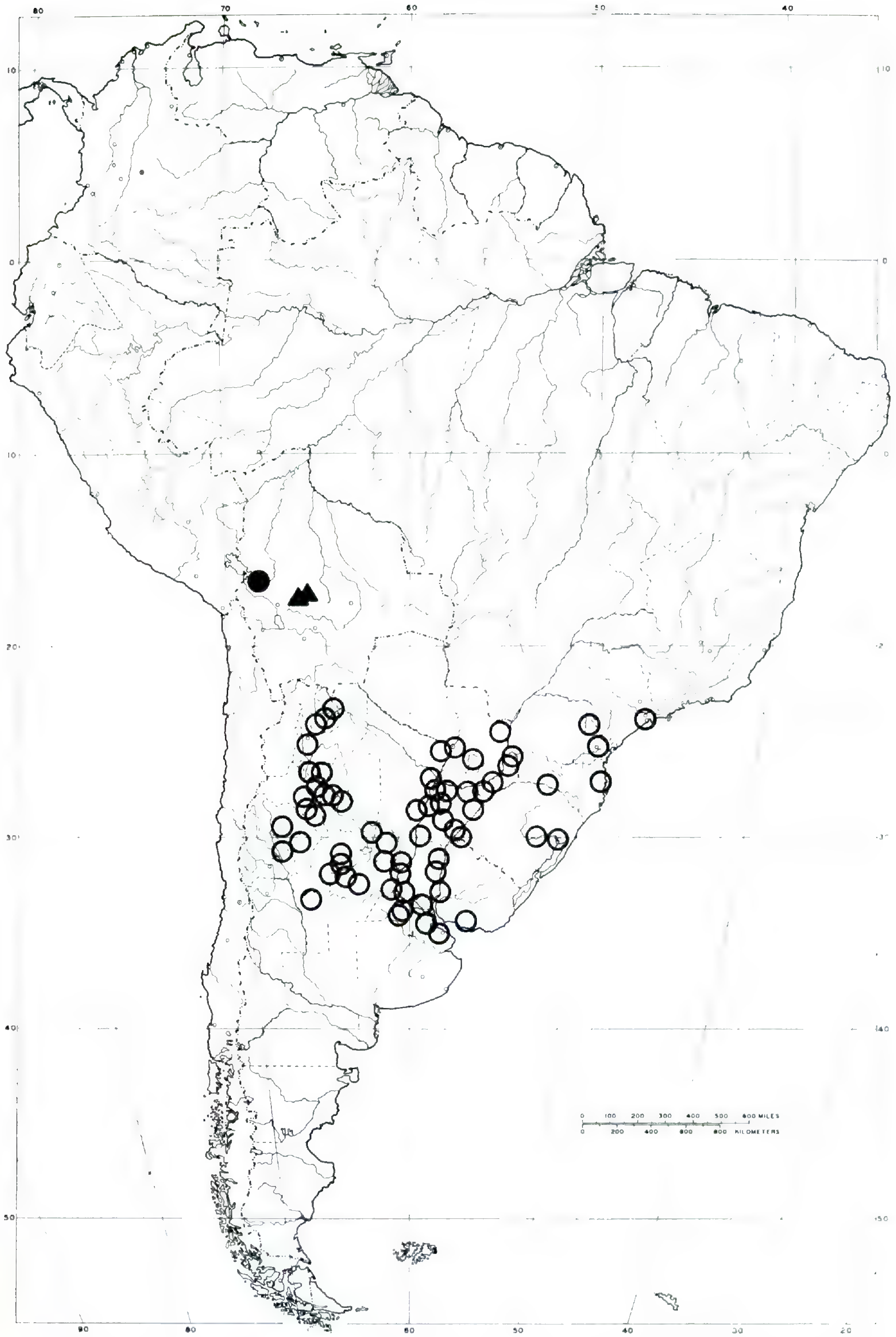


FIGURE 233. Ranges of *Oenothera indecora* subsp. *bonariensis* (circles), *O. indecora* subsp. *boliviensis* (dot), and *O. pseudoelongata* (filled triangles).

thick. Seeds 1.1–1.5 mm long, 0.5–0.7 mm thick. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 11 Aug. 1972. Source: Brazil, Rio Grande do Sul, Pelotas, 1966, *E. J. Hackbart* (MO-2155412, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 236): From the state of São Paulo to Rio Grande do Sul in Brazil; in the departments of Salto, Rivera, Paysandú, Soriano, Cerro Largo, Maldonado, Montevideo, Canelones, Florida, and Flores in Uruguay; and in the provinces of Misiones, Corrientes, Entre Ríos, Buenos Aires, Formosa, Chaco and Santa Fé in Argentina.

Specimens examined from cultivated plants:

BRAZIL. RIO GRANDE DO SUL: Pelotas, *Hackbart in 1966* (CTES, DUSS, M, MO), *in 1967** (CTES, DUSS, M, MO).

URUGUAY. MONTEVIDEO: Carrasco, *Hecht 1964–67** (CTES, DUSS, M, MO). FLORIDA: *Hecht 1964–31** (CTES, DUSS, MO).

ARGENTINA. ENTRE RÍOS: Concórdia, *Burkart 23063** (CTES, DUSS, M, MO, SP). Dep. Concórdia, Ayui, *Burkart 23423** (DUSS, M, MO). Concepción del Uruguay, *Burkart in 1967** (CTES, DUSS, M, MO).

Representative specimens examined:

BRAZIL. SÃO PAULO: Jordão, 1,300 m, *Santos* (R); *Leite 3512* (GH). SANTA CATARINA: S. Joaquim, 1,300 m, *Reitz & Klein 7977* (G). Perto de Painel between Lajes and S. Joaquim, 800–1,000 m, *Lutz in 1949* (R). Campo dos Padres, *Rambo 60069* (B). RIO GRANDE DO SUL: S. Angelo, *Schwarzer in 1900* (S). Farroupilha, *Camargo 2636* (B); *Rambo 40278* (LIL). Bom Jesus, *Rambo 34863* (LIL, S). Caxias do Sul, *Sehnem 3994* (B, SI). Rio Caí near Pôrto Alegre, *Rambo 43868* (LIL). Caçapava, *Palacios & Cuezzo 1407, 1448* (LIL). Passo do Socorra near Vacaria, *Rambo 51617* (S, US). Canôas near Pôrto Alegre, *Palacios & Cuezzo 278* (LIL). São Leopoldo, *Eugenio 204* (NY). Bento Gonçalves, *Santos 2616* (R). Serra dos Taypes, *Schwacke 2597* (R).

URUGUAY. SALTO: *N.N.* (K). PAYSANDÚ: Km 437 at Ruta 3 near Suelo Chapicuy, *Millot 494* (MVFA). SORIANO: Est. Mauriño near Mercedes, *N.N. 91* (POM). RIVERA: Cunapiru, *Wright in 1928* (BM). FLORES: Between Río Yi and Arroyo Mariacho, *Rosengurtt B1521* (LIL, POM). FLORIDA: *Rosengurtt B703* (BAA). Mansavillagra, *Rosengurtt B1657* (LIL, POM). CANELONES: Dunes near La Floresta, *Steer in 1923* (HBG). MONTEVIDEO: *Gibert 86a, 341* (K); *Orbigny in 1829* (P). Quinta Narelo, *Fruchard in 1876* (P). Carrasco, *Munz 15451* (NY, POM). CERRO LARGO: Between Paso Cruz and Río Tacuari, *Arrillaga 2341* (MVFA). Between Río Negro and Arroyo Aceguá, *Rosengurtt 820* (POM). MALDONADO: Solís, *Osten 21653* (BREM); *Cunningham in 1867* (K).

ARGENTINA. FORMOSA: *Jörgensen 3025* (POM, SI). CHACO: Las Palmas, *Jörgensen 2487* (GH, SI, US), *2489* pro parte (POM). SANTA FÉ: Mocovi, *Venturi 275* (SI). Chacras between Carcaraña and Cañada de Gomez, *Berndt 5166* (CORD). Rafaelo near Castellanos, *Terribile 387* (LIL). MISIONES: Puerto Segundo near Iguazú, *Montes 10363* (CORD, LP). El Soberbio near Guaraní, *Crisci 297* (LP). CORRIENTES: Gral. Paz, *Krapovickas & Cristóbal 11836* (CTES, UC); *Schwarz 321* (LIL). Dep. Capital, Arroyo Riachuelo at Ruta 12, *Krapovickas & Cristóbal 13783* (BAA, BAB, C, CTES, LP, MO). La Cruz near San Martín, *Parodi 12368* (BAA). Juan Pujol near Monte Caseros, *Ibarrola 2323* (LIL). Est. Tranqueras near Monte Caseros, *Nicora 5187* (CTES). Vicinity of Concepción, *Ibarrola 022, 431, 546* (LIL). Vicinity of Paso de los Libres, *Schinini 7699* (CTES, MO); *Huidobro 3815, 3837* (LIL). Est. Santa Teresa near Mburucuyá, *Pedersen 93* pro parte (C). Vicinity of Ituzaingó, *Pierotti 6227, 6195, 6174* (LIL). Santo Tomé, *Ibarrola 1438* (LIL, NY); *Krapovickas et al. 21150* (CTES, MO). Mercedes, *Millan 334* (POM). Between Ruta 27 and Río Corrientes near Esquina, *Krapovickas et al. 27111* (CTES, MO). ENTRE RIOS: Villaguay, *Meyer 11187* (LIL). Colón, *Meyer 10657* (LIL). Concordia, *Burkart 26731, 28763* (MO); *Cabrera 19261* (LP). Concepción del Uruguay, *Lorentz 514* (BREM, CORD, GOET, K, W). Est. La Selmira near Concordia, *Pedersen 7260* (C). Federación, *Crovetto 4889* (BAB). BUENOS AIRES: Est. San Juan, 30 km S of Buenos Aires, *Eyerdam et al. 23037* (SI). Cajón, *Cabrera 6430* (LP). Delta del Paraná, Arroyo Carabales, *Burkart 4316* (CTES).

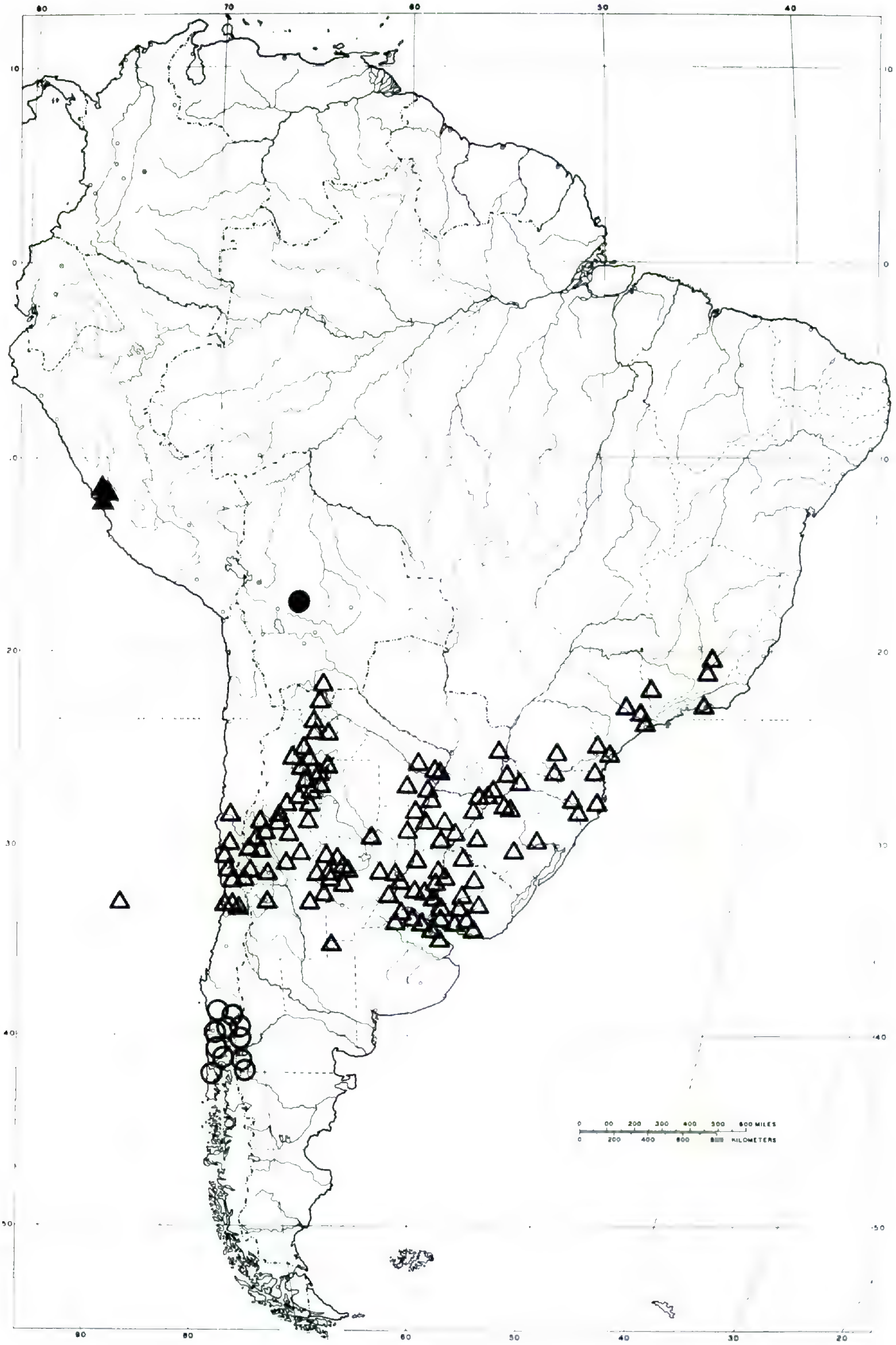


FIGURE 234. Ranges of *Oenothera affinis* (hollow triangles), *O. villaricae* (circles), *O. brevipetala* (dot), and *O. featherstonei* (filled triangles).

In habit, *O. parodiana* subsp. *brasiliensis* resembles the chromosomally homozygous *O. ravenii* very closely. Analysis of the complexes present in this subspecies has shown that it is predominantly derived from *O. ravenii* and *O. indecora*, with some introgression from *O. affinis* and *O. longiflora*, as indicated among other points by the length of the floral tube. Transitional forms with subsp. *parodiana* occur frequently in the zone of contact.

29. **Oenothera verrucosa** Johnston, Contr. Gray Herb. 70: 77. 1924.—FIGS. 12, 149, 185, 209.

Erect annual herb, not forming a rosette, simple or branched from the base upward, 1.5–5 dm tall. Plant moderately to sparsely strigillose, moderately to sparsely villous, and sparsely glandular-pubescent. Cauline leaves very narrowly elliptic to elliptic or lanceolate, acute, attenuate to rounded at the base, only the lowermost short-petiolate, the remainder sessile, 4–8 cm long, 0.5–1.5 cm wide; bracts narrowly lanceolate to lanceolate, acute, rounded to truncate at the base, sessile, 3–5 cm long, 0.5–1.2 cm wide, longer than the capsules they subtend; leaves plane to slightly undulate at the margins, remotely serrulate, the teeth blunt. Inflorescence simple or branched. Floral tube 0.6–1.1 cm long. Buds oblong to broadly elliptic in outline, yellowish, often flushed with red, 0.3–0.6 cm long, 2.5–3.5 mm thick; apices of the sepals 0.5–1 mm long, erect. Petals very broadly obovate, 0.3–1 cm long. Anthers 1–2.5 mm long. Filaments 2.5–4 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 0.8–1.5 cm long. Stigma lobes 1.5–2 mm long. Ovary 0.6–1 cm long. Capsule 1.5–2.5(–3) cm long, 2.5–3.5 mm thick, erect, apparently petiolate; valves spreading apart after dehiscence, not curving. Seeds elliptic in outline, 1.5–1.7 mm long, 0.7–0.8 mm thick, dark brown to almost black. Self-pollinating. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: March–April.

Type: Peru, Dep. Arequipa, ravines and rocky slopes, Pampa, southern slopes of Chachaní Mountain north of Arequipa, 3,660 m, Mar. 1920, *Mr. and Mrs. F. E. Hinkley 17* (GH, holotype; BAS, isotype).

Distribution (Fig. 238): Known only from the Andes of the department of Arequipa, southern Peru, at elevations from 2,400–3,700 m.

Specimens examined from cultivated plants:

PERU. Dep. Arequipa: Quebrada de San Lázaro, 5–6 km NNE of Arequipa below the El Misti, sandy places W of the river, 2,600 m, *Santarius 2068**, *2071*, *2073** (DUSS; *2068*, *2073* also M; *2068* also CTES, MO).

Additional specimens examined:

PERU. AREQUIPA: Near Arequipa, *Stafford D10* (K); 2,700 m, *N.N. in 1954* (RSA); 2,400–2,600 m, *Pennell 13174* (F, GH, K, NY, S, US, USM); *Nuñez 97* (USM); *N.N. in 1925* (US-1231003). Baño de Jesus, 2,600–2,700 m, *Ferreyra 14252* (USM). Slopes of the Misti between Yura and Arequipa, *Sandeman 3960* (K). Mountains near Yura, 2,575–2,600 m, *Vargas 7974* (LIL, MO, RSA). Quebrada San Lázaro, 2,800 m, *Munz 15483*, *15527*, *15528* (POM). Chihuata 20 km E of Arequipa, 2,600 m, *Munz 15540* (POM, US). Characato near Arequipa, 2,400–2,600 m, *Vargas 8043* (LIL).

Oenothera verrucosa seems to be a declining species which has found a last refuge in the Andes of Arequipa. It evidently participated in the origin of the derivative complex heterozygote *O. arequipensis*, which occurs at low elevations along the coast of southern Peru and northern Chile. Possibly *O. verrucosa* at one time occupied much of the same area as *O. arequipensis*, but more likely that derivative species was simply able to expand its range into the newly developed very arid regions during and after the Pleistocene, whereas *O. verrucosa* became confined to its present very limited area of distribution.

An important characteristic of *O. verrucosa* is the stipitate appearance of its erect capsules, owing to their abrupt narrowing toward the base. *Oenothera verrucosa* and the following two species, *O. coquimbensis* and *O. arequipensis*, are obligate annuals and do not form a rosette. Responding to the short period of growth available to them, they elongate rapidly after forming only a few leaves and form their first buds only 4–5 weeks after germination. In cultivation, all other species require a much longer time for the initiation of their first buds.

30. **Oenothera coquimbensis** Gay, Fl. Chil. 2: 331. 1847.—Figs. 150–151, 186.

O. grandidentata Philippi, Linnaea 33: 68. 1864. LECTOTYPE: Chile, Prov. Atacama, near Caldera, Dec. 1854, *R. A. Philippi* (SGO-052835, GH, NY and POM photographs); Munz, Amer. J. Bot. 22: 658. 1935.

O. coquimbensis Gay var. *grandidentata* (Philippi) Reiche, Anales Univ. Chile 98: 476. 1897; Fl. Chile: 258. 1898.

Onothera albicaulis Pursh var. *tigrina* H. Lév. subvar. *coquimbensis* (Gay) H. Lév., Monogr. Onoth. 345. 1909; Bull. Acad. Int. Géogr. Bot. 19: 305. 1909.

Raimannia coquimbensis (Gay) Sprague & Riley, Bull. Misc. Infor. 1921: 200. 1921.

Erect annual herb, not forming a rosette, simple or branched from the ground upward, 0.5–5 dm tall. Plants densely to moderately strigillose, moderately long- and short-villous. Cauline leaves very narrowly elliptic to elliptic or lanceolate to narrowly ovate, acute, acute to truncate at the base, sessile, 5–8 cm long, 0.5–1.5 cm wide; bracts narrowly lanceolate to narrowly ovate, acute, truncate to subcordate at the base, subsessile, 2–6 cm long, 0.5–1.5 cm wide; leaves usually plane at the margins, irregularly and coarsely toothed or ± regularly and deeply toothed, sometimes doubly so, often flecked with dark reddish brown. Inflorescence simple or branched. Floral tube 1–3 cm long. Buds broadly elliptic to narrowly ovate in outline, yellowish, often striped with red at the junction of the sepals with the floral tube, 0.5–1.3 cm long, 3–3.5 mm thick; apices of the sepals 1–3 mm long, erect or divergent. Petals very broadly obovate, 0.8–2 cm long. Anthers 2.5–6 mm long. Filaments 5–13 mm long. Style held above the anthers in most individuals, occasionally shorter and then the anthers shedding directly on it at anthesis, 2–4 cm long. Stigma lobes 2.5–4 mm long. Ovary ca. 1 cm long. Capsule 1–2.5 cm long, 2.5–3.5 mm thick, ± erect or spreading obliquely from the stem, often somewhat enveloped by the subtending bract. Seeds narrowly elliptic in outline, 1.2–1.6 mm long, 0.4–0.5 mm thick. Self-compatible but mostly outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents* at meiotic metaphase I). Flowering time: September–November.

Type: Chile, Prov. Coquimbo, on dunes at the edge of the sea, very rare, vicinity of La Serena, Dec. 1836, *Cl. Gay 520* (P, holotype; F, GH, K, P, isotypes).

Distribution (Fig. 239): Sandy flats and dunes near the coast in the semideserts of Chile from Antofagasta to Purén, Malleco Province.

Specimens examined from cultivated plants:

Grown from seeds of a herbarium specimen in 1973 at MO. Source: Chile, Prov. Atacama, Dep. Freirina, road from Chañaral de Aceituna to Bahía Carrizal at km 6, *Marticorena, Rodríguez, Weldt 1846** (CONC-36723).

Additional specimens examined:

CHILE. ANTOFAGASTA: Base of hills just SE of La Chimba, *Johnston 3640* (GH, US). ATACAMA: *Geisse in 1885–1887* (NY); *Morong 1141, 1162, 1231, 1264* (NY), *1285* (K, MICH, NY, US). Chañaral, *Ricardi 2258* (CONC). Hills back of El Barquito at Puerto de Chañaral, *Johnston 4772* (CH). Vicinity of Caleta Pan de Azúcar, dunes on point just S of the Caleta, *Johnston 5839* (F, GH, K, LIL, S, US). Road from Chañaral de Aceituna to Bahía Carrizal at km 6, *Marticorena 1846* (CONC). Carrizal, *N.N. in 1885* (SGO-052891). Huasco, *Monypenny 46* (CONC). Algarrobal at Pan-Amer. Highway, *Cabrera 12649* (LP). *Ricardi 4410-795* (CONC). 1 km S of Huasco, *Böcher et al. 540* (C). Vicinity of Copiapó, 370 m, *Johnston 4990, 5030* (GH); *Philippi 1726* (SGO); *N.N. in 1885* (SGO-052892). Pan-Amer. Highway between Caldera and Chañaral at km 18, *Ricardi et al. 1304-B* (CONC). Between Copiapó and Vallenar at km 55, *Ricardi et al. 1511* (CONC). At km 40, *Ricardi 2210* (CONC). Morro de Copiapó, sandy washes along a stream near the sea, *Worth 16185* (K, UC). Quebrada de Chanchoquin near Copiapó, *Gigoux in 1895* (GH). Travesia, *Kohler 153* (CONC); *Jiles 2160* (CONC); *N.N.* (SGO-052890). Caldera near Copiapó, *Gigoux in 1894* (GH); *Philippi 1726b, 1726c, 1724* (SGO), *in 1885* (SGO-052889). Piedra Colgada, *Philippi in 1885* (SGO-052893, SGO-052887). Bandurrias, *Geisse 1726a* (SGO). Pojonales, *Geisse in 1888* (SGO). COQUIMBO: *Gay in 1838* (P); *Reiche in 1909* (SGO-052879); *Jaffuel 2679* (GH); *Philippi 785* (US); *Elliott 85* (K). Between La Serena and Punta de Teatinos, *West 3919* (GH, MO, UC). La Serena, Choros Bajos, *Marticorena 1694* (CONC). Between Herradura and Coquimbo, *Skottsberg in 1917* (NY, S). Dunes between Tongoy and Guanaqueros near Ovalle, *Gleisner 5* (CONC). Est. Talca near the sea, dep. Ovalle, *Jiles 1425* (CONC, S). Quilimarí, *in 1862* (SGO-052833). VALPARAÍSO: Valparaíso, *Calvert in 1914* (BM). MALLECO: Near Purén, *N.N. 1229 in 1838* (SGO-052834).

Cultivated specimens:

Botanical Garden, Leningrad, seeds from Chile, Prov. Atacama, from sandy plains near Huasco, sent by Cuming, *in 1847* (LE; as *O. glauco-virens* F.M.).

Oenothera coquimbensis is totally distinct from *O. verrucosa* in its characteristic pattern of toothing of the leaves, its larger flowers, and its different mode of capsular dehiscence, in which the valves curve inward. In addition, the capsules usually spread obliquely from the stems instead of standing erect and are often partially enfolded by their subtending bract. Finally, the seeds are shorter and narrower than those of *O. verrucosa.*

Within *O. coquimbensis* there are two distinctive variants, but these are so completely joined by intermediate forms that it does not seem desirable to accord them formal taxonomic recognition. One has extraordinarily deeply toothed leaves in which the teeth are very narrow and long and often also secondarily toothed. The second has relatively wide leaves which are merely coarsely serrate.

Oenothera coquimbensis, *O. arequipensis*, and to some extent, *O. nocturna*, species of the coastal deserts of Peru and Chile, appear only in years of ample rainfall, and thus represent a distinctive ecological type within subsect. *Munzia.* The evolution of these deserts, and consequently of the species that inhabit them, is a phenomenon of Late Pleistocene and Recent time (Raven & Axelrod, 1974).

31. **Oenothera arequipensis** Munz & Johnston, Contr. Gray Herb. 75: 20. 1925. —Figs. 152, 187–188.

O. laciniata Hill var. *limensis* Munz & Johnston, Contr. Gray Herb. 75: 20. 1925. TYPE: Peru, Dep. Lima, sandy lomas along the sea near Lurín, 23 Sep. 1925, *J. F. Macbride 5950* (F-536954, holotype, NY, photograph; GH, K, US isotypes).
O. laciniata var. *nocturna* (Jacq.) Munz, Amer. J. Bot. 22: 656. 1935, pro parte.
O. laciniata sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 537. 1941, pro parte.
O. verrucosa sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 540. 1941, pro parte.

Erect annual herb, not forming a rosette, usually branched near the base, 1–3.5 dm tall. Plant densely to sparsely strigillose and densely to sparsely appressed- or erect-villous, sometimes almost glabrous. Cauline leaves narrowly elliptic to narrowly oblanceolate, acute, gradually narrowed to the short petiole, 2–10 cm long, 0.5–2 cm wide; bracts narrowly elliptic to narrowly ovate, acute, acute at the base, sessile, 2.5–5 cm long, 0.5–1.5 cm wide, longer than the capsules they subtend; leaves plane to slightly undulate at the margins, usually deeply sinuate. Inflorescence usually branched. Floral tube 1–3 cm long. Buds oblong in outline, yellowish, sometimes flushed with red, 0.3–0.8 cm long, 2–4 mm thick; apices of the sepals 1–2 mm long, erect or divergent. Petals very broadly obovate, 0.4–1.5 cm long. Anthers 2–3.5 mm long. Filaments 5–7 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.3–4 cm long. Stigma lobes 2–3.5 mm long. Ovary ca. 1 cm long. Capsule 1.5–3 cm long, 2.5–4 mm thick, tapering at both ends and usually appearing pedicellate, mostly erect; valves spreading apart in dehiscence. Seeds elliptic to nearly rotund in outline, 1–1.3 mm long, 0.6–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: September–November.

Type: Peru, Dep. Arequipa, sandy slope, desert hills near Mollendo, 17 Nov. 1923, *A. S. Hitchcock 22403* (US-1,196.655).

Distribution (Fig. 231): In the lomas of the Pacific coastal deserts and semideserts of Peru from the department of Libertad to Tacna, ascending to 2,700 m elevation in the vicinity of Lima; in Chile only known from Tocopilla in the province of Antofagasta.

Specimen examined from cultivated plants:

PERU. LIMA: Prov. Huarochirí, Huascamarca near Santiago de Tuna, 2,700 m, *Encarnación 346** (DUSS).

Additional specimens examined:

PERU. LA LIBERTAD: Cerro Campana near Trujillo, 350 m, *López 0907* (US). Cerro Cabezon near Trujillo, 400–500 m, *Weberbauer in 1940* (USM). ANCASH: Lomas de Casma near Santa, 250–300 m, *Ferreyra 8039* (US). LIMA: Lima, *Cuming 1079* (K); *Soukup 2158* (F); *Mathews* pro parte (K). Lomas near Barranco, 50–100 m, *Weberbauer 5703* (F, GH, US). San Agustín, *Asplund in 1940* (RSA). Lomas de Atocongo, 300–400 m, *Ferreyra 2448* (US). Lomas de Lachay near Chancay, *Cerrata 3825* (MO). Pasomayo near Chancay, 300 m, *Stork 9353* (GH, K, UC). Hacienda Desagravio near Huaura, *Goytizolo in 1943* (USM-12875). AREQUIPA: Arequipa, *in 1892* (GH). Mollendo near Islay, 300 m, *Ferreyra 12102* (USM); *Mexia 04167* (MO, UC, US); *Stafford 279* (K). Hillside directly back of the port, *Johnston 3556, 6303* (GH); *Worth & Morrison 15764* (GH, K, UC). Slopes of the Misti, *Cárdenas & Rodríguez 3* (F). Prov. Caravelí, Lomas de Jahuay, km 534 between Nazca and Chala, 300–400 m, *Ferreyra 1396* (USM). Lomas de Capac near Chala, 300 m, *Ferreyra 1433* (USM). Between Tambo and Posco, 300–550 m, *princess Therese of Bavaria 233* (M). Lomas de Camaná, 600–700 m, *Ferreyra 6440* (US, USM). Cerro los Cerillos, W of Pan Am. High-

FIGURE 235. Ranges of *Oenothera stricta* subsp. *argentinae* (circles), *O. montevidensis* (hollow triangles), *O. pseudolongiflora* (filled triangle), and *O. hechtii* (dot).

way, 52 km S of Nazca, km 500, 650 m, *Rahn 130* (C). Along Pan-Amer. Highway, 28.9 km NW of Chala, 240 m, *Rahn in 1957* (C). Capac, *Scolnik 1019* (CORD, LIL, RSA). MOQUEGUA: Lomas de Ilo near Mariscal Nieto, 600–700 m, *Ferreyra 12577* (BM, MO, USM). Lomas de Mostacilla near Ilo, 300 m, *Vargas 8598* (LIL). TACNA: Morro de Sama, 450 m, *Delarte 7315* (RSA).

CHILE. ANTOFAGASTA: Dep. Tocopilla, steep hillside ca. 6 km north of port and about opposite Caleta Duendes, *Johnston 3602* (GH, S, US). Tocopilla, *Jaffuel 2554* (GH).

The close similarity in general aspect between *O. arequipensis* and *O. verrucosa* led Munz (1935) to combine them as a single species ten years after first describing the former. Notwithstanding this, there are fundamental differences between them. *Oenothera arequipensis* is branched to a greater extent and has sinuate leaves and seeds that are much broader. Moreover, *O. verrucosa* is chromosomally homozygous and occurs only at elevations greater than 2,000 m in the department of Arequipa; *O. arequipensis* is a complex heterozygote and inhabits mainly the sea-level lomas of the coastal deserts of Peru and northernmost Chile.

No hybrids involving *O. arequipensis* have yet been analyzed to determine the genomes involved in the formation of this species. Nevertheless, it probably contains a genome derived from *O. verrucosa,* since the resemblance between these two species is much too close to be attributed to chance. Its second genome is probably derived from *O. laciniata* subsp. *pubescens,* which ranges south at least to the Peruvian Departments of Lima and Junín. At the very least, the second genome of *O. arequipensis* must contain a strong admixture of genes from this entity, as indicated by the sinuate leaves and the seeds which are often nearly rotund in outline. On the other hand, *O. arequipensis* never exhibits the nodding buds of *O. laciniata.*

Oenothera arequipensis provides an impressive example of the reticulate relationships between the subsections of sect. *Oenothera,* linking a highly derived South American species with a "late arrival" in South America as a complex heterozygote of rather local distribution in a habitat that is clearly marginal for the genus as a whole.

32. **Oenothera grisea** Dietrich, sp. nov.—FIGS. 86–87, 154.

Herba annua erecta, non rosulata, multiramosa, 2–5 dm alta, nonnisi denseque strigulosa, caulibus foliisque ut videtur griseo-viridibus. Folia caulina anguste elliptica vel anguste lanceolata, acuta, basi acuta vel rotundata, sessilia, 5–10 cm longa, 0.8–1.2 cm lata; bractea lanceolata vel ovata, acuta, basi truncata vel subcordata, sessilia, 2–3 cm longa, 1–1.5 cm lata; folia manifeste ad margines undulata, irregulariter obtuseque serrata. Inflorescentia ramosa. Tubus floralis 1–1.5 cm longus. Gemmae ambito oblongae vel ellipticae, 0.8–1 cm longae, 3–4 mm crassae, griseo-virides; apices sepalorum 1–1.5 mm longi, divergentes. Petala latissime obovata, 0.8–1.2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 6–7 mm longum. Capsula 2–2.5 cm longa, 2.5–3.5 cm crassa. Semina ambito elliptica, 1.3–1.5 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, usually with many branches arising from the base upward, 2–5 dm tall. Plants exclusively and densely strigillose, the stems and leaves appearing gray green. Cauline leaves narrowly elliptic to narrowly lanceolate, acute, acute to rounded at the base, sessile, 5–10 cm long, 0.8–1.2 cm wide; bracts lanceolate to ovate, acute, truncate to subcordate at the

base, sessile, 2–3 cm long, 1–1.5 cm wide; leaves evidently undulate along the margins, irregularly serrate with blunt teeth. Inflorescence branched. Floral tube 1–1.5 cm long. Buds oblong to elliptic in outline, 0.8–1 cm long, 3–4 mm thick, gray green; apices of the sepals 1–1.5 mm long, divergent. Petals very broadly obovate, 0.8–1.2 cm long. Anthers ca. 4 mm long. Filaments 5–6 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.5–2.5 cm long. Stigma lobes ca. 3 mm long. Ovary 6–7 mm long. Capsule 2–2.5 cm long, 2.5–3.5 cm thick. Seeds elliptic in outline, 1.3–1.5 mm long, 0.5–0.7 mm thick, brown. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: December–March.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 17 Aug. 1971. Source: Chile, Prov. Valparaíso, Las Ventanas, end of 1965, *L. Constance* (MO-2155203, holotype; DUSS, M, isotypes).

Distribution (Fig. 232): Known only from the dunes at Concón, province of Valparaíso, Chile.

Specimens examined from cultivated plants:

CHILE. VALPARAÍSO: Las Ventanas, *Constance in 1965** (DUSS, M, MO).

Additional specimens examined:

CHILE. VALPARAÍSO: Ritoque, dunes near Concón, *Poulson in 1952* (C). Quinteros near Concón, *Philippi in 1866* (W). Dunes near Concón, *Jaffuel 3956* (GH); *Zöllner 6086* (L).

The complex heterozygote *O. grisea* is similar in habit to *O. coquimbensis*, but can be distinguished by its exclusively strigillose pubescence; plants of *O. grisea* are grayish in appearance. This species grows poorly in cultivation, and the flowers often drop off prematurely or do not form any pollen. For this reason, it has not yet been possible to analyze its genetic constitution fully. However, one genome seems to have been derived from the *odorata*-complex of *O. stricta* because hybridization with *O. odorata* produces an F_1 generation in which one type is very similar to *O. odorata*. The second genome may have been derived from the chromosomally homozygous *O. coquimbensis*, as suggested by the morphological similarity between that species and *O. grisea*. Both of the putative parents, *O. coquimbensis* and *O. stricta*, grow in the same area as *O. grisea*. The restricted distribution of *O. grisea*, which occurs only on the dunes at Concón near Valparaíso, seems to indicate a very recent origin for this species.

33. **Oenothera featherstonei** Munz & Johnston, Contr. Gray Herb. 75: 19. 1925. —FIGS. 153, 189.

Erect annual or perhaps sometimes perennial herb with arcuate side branches, to 5 dm tall. Plants exclusively strigillose. Cauline leaves very narrowly elliptic to elliptic, acute, narrowly cuneate at the base, short-petiolate, 3–5 dm long, 0.8–1.2 cm wide; bracts narrowly elliptic to lanceolate, acute, attenuate at the base, 2.5–4 cm long, 0.5–1 cm wide; leaves plane at the margins, irregularly serrate, the teeth sharp or blunt. Inflorescence branched. Floral tube 3–4 cm long. Buds lanceolate in outline, 2–3 cm long, 5–9 mm thick, yellowish;

FIGURE 236. Ranges of *Oenothera bahia-blancae* (filled triangles), *O. parodiana* subsp. *brasiliensis* (circles), *O. elongata* (dots), and *O. tucumanensis* (hollow triangles).

apices of the sepals 2–4 mm long, divergent. Petals very broadly obovate, 2.5–4 cm long. Anthers 8–12 mm long. Filaments 16–24 mm long. Style long, the stigma elevated well above the anthers at anthesis, 4–7.5 cm long. Stigma lobes 3–7 mm long. Ovary 1.5–2 cm long. Capsule 2–2.5 cm long, 2.5–3 mm thick. Seeds elliptic in outline, 1.3–1.5 mm long, 0.6–0.7 mm thick, dark brown to almost black. Self-compatible but outcrossing. Gametic chromosome number, $n = 7$ (7 bivalents*, ring of 8 and 3 bivalents** or ring of 10 and 2 bivalents*** at meiotic metaphase I). Flowering time: February–May.

Type: Peru, Dep. Lima, sprawling on disintegrated granite slope, Matucana, 12 Apr.–3 May 1922, *J. F. Macbride & Featherstone 270* (F-516,803, NY photograph; G, GH, K, isotypes).

Distribution (Fig. 234): Apparently only in the vicinity of Matucana, department of Lima, Peru, at elevations of 2,000–2,500 m.

Specimens examined from cultivated plants:

PERU. LIMA: Prov. Huarochirí, at km 63 of the railroad from Lima to Oroya, between Surco and Puente Quitasombrero, 2,050–2,100 m, *Encarnación in 1974**, **, *** (DUSS).

Additional specimens examined:

PERU. LIMA: At Lima-Oroya railway between Surco and Matucana, 2,000–2,400 m, *Weberbauer 5217* (F, G, GH, POM, US). Matucana, 2,400 m, *Asplund 10994* (RSA, UPS); *Rauh in 1954* (RSA). Vicinity of Surco, *Ferreyra 9657* (USM). Puruchuca near Matucana, *Mathews 492* (K). Near Canta, 2,200–2,500 m, *Acleto 605* (USM). *N.N. in 1950* (USM). Without exact locality: *Martinet in 1878* (P), *Martinet 71* (P).

Oenothera featherstonei has flowers as large as those of *O. odorata* and *O. ravenii*. Its area of distribution presumably extended to lower elevations along the coast of Peru during the Pleistocene. *Oenothera nocturna*, its complex heterozygote derivative, still coexists in these areas with *O. laciniata* subsp. *pubescens*. The spread of *O. nocturna* may have played a role in limiting the range of *O. featherstonei* to its present very limited area. Plants with 8 or 10 rings of chromosomes at meiotic metaphase I may represent hybrids between *O. featherstonei* and *O. nocturna*. On the basis of its nearly black seeds and strigillose pubescence, which gives the plants a grayish hue, one might hypothesize that *O. featherstonei* may have been derived from an ancestral form similar to *O. peruana* (series *Renneria*), the least specialized of all species of subsect. *Munzia*.

34. **Oenothera nocturna** Jacq., Coll. 3: 205. 1789; Icon. Pl. Rar. 3: 3, *tab.* 455. 1791.—FIGS. 155, 190, 224.

O. albicans Lam., Encycl. Méth. 4: 552, *tab. 279, fig. 2.* 1797. TYPE: not seen. The illustration in Encycl. *tab. 279* represents the species here described.

O. prostrata Ruiz & Pavón, Fl. Peruv. Chil. 3: 79, *tab. 315.* 1802. LECTOTYPE: Peru, Dep. Lima, common in the provinces of Lima and Chancay, *J. Dombey* (P).

Onagra nocturna (Jacq.) Moench, Suppl. Meth. Pl. 287. 1802.

Onothera polymorpha H. Lév. race *longiflora* (Jacq.) H. Lév. var. *nocturna* (Jacq.) H. Lév., Monogr. Onoth. 364. 1909; Bull. Acad. Int. Géogr. Bot. 19: 324. 1909.

Raimannia nocturna (Jacq.) Sprague & Riley, Kew Bull. 1921: 201. 1921.

Oenothera laciniata Hill var. *nocturna* (Jacq.) Munz, Amer. J. Bot. 22: 656. 1935.

O. laciniata sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 537. 1941, pro parte.

Erect annual to perhaps sometimes perennial herb, forming a weak rosette, well branched near the base, 3–6 dm tall. Plants exclusively strigillose. Cauline

leaves elliptic or narrowly lanceolate to lanceolate, acute, narrowly cuneate at the base, short-petiolate, 4–6 cm long, 0.5–1.5 cm wide; bracts narrowly elliptic to lanceolate, acute, acute at the base, 1.5–3 cm long, 0.5–1 cm wide; leaves plane to slightly undulate at the margins, ± regularly sinuate. Inflorescence usually branched. Floral tube 1.5–2.5 cm long. Buds oblong in outline, 0.5–1 cm long, 3–4 mm thick; apices of the sepals 1.5–2.5 mm long, divergent. Petals very broadly obovate, 1–1.5 cm long. Anthers 4–7 mm long. Filaments 6–13 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2–3.2 cm long. Stigma lobes 3–5 mm long. Ovary 1–1.3 cm long. Capsule 1.8–2.5(–3) cm long, 2.5–3.5 mm thick. Seeds elliptic to broadly elliptic in outline, 1.3–1.8 mm long, 0.8–0.9 mm thick, dark brown to almost black. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: At high elevations, February–June; at low elevations, September–November.

Neotype: Jacq., Icon. Pl. Rar. 3: *tab. 455.* 1795. No specimen collected before 1792 seems to have persisted, but the identity of this taxon is made clear by the plate selected as the neotype, and by the following two old cultivated specimens labeled with this name: Hort. Kew, 1792 (BM). Cult. Hort. Paris, Oct. 1815, Herb. J. Gay (GH, K). It was said to be from the Cape of Good Hope, but no African material has been seen; the original seeds undoubtedly came from the vicinity of Lima or elsewhere in Peru, to which the species is endemic.

Distribution (Fig. 239): Predominantly at lower elevations in the departments of La Libertad, Lima, Huancavelica, and Ancash, Peru, but ascending into the mountains along river valleys to 3,200 m elevation.

Specimens examined from cultivated plants:

PERU. LIMA: Valley of Río Rimac, at the road and on dry slopes, between the road (km 74.9–76.1) and the railroad (km 99–100) from Lima to Oroya, near Matucana, ca. 2,200 m, *Santarius 2327**, *2328**, *2333** (DUSS, MO: *2328* also CTES, M).

Additional specimens examined:

PERU. LA LIBERTAD: In valley between Pacasmayo and railhead, 2,130 m, *Forbes in 1912* (BM). Trujillo, Barranza, 60 m, *Sagástegui 7857* (CTES, MO). ANCASH: Recuay near Marca, 2,600 m, *Gómez 38* (USM). Carancayo in valley Fortaleza near Bolgnesi, 2,600 m, *Cerrate 12188* (BM, USM). Taclán, 3,050–3,100 m, *Proaño 87* (USM). LIMA: Lima, *Savatier 1395* (K), *Martinet 40 (882)* (P, US); *Anderson in 1852* (S); *Mathews 493* (K). San Agustín, *Asplund 13824* (RSA). San Boskobo, 120–240 m, *Saunders 163* (BM). Lomas de Lurín, 400–500 m, *Ferreyra 9536* (BM, USM). Lomas de Atocongo, 300–400 m, *Ferreyra 0172, 2062, 12478* (USM); *Aguilar in 1948* (USM); *Pennell 14777* (F); *Vargas et al. 9296* (GH, K, UC). Chancay, *Dombey 727* (G, L, P). *Vargas 4710* (MO). Ruins of Cajamarquilla near Chancay, 300–400 m, *Ferreyra 2838* (USM). Supe, near Chancay, 100 m, *Goodspeed et al. 17361* (UC). Lomas de Lachay, between Chancay and Huacho, 400–500 m, *Ferreyra 8770, 11503* (USM); *Infantes 2128* (LIL); *Cerrate 856* (BM, USM). Madalena near Lima, *Née* (F). San Isidro, *Raimondi 6115* (USM). Miraflores, *Maisch 13727* (USM). Amancae, *Jaffuel 3934* (GH). River Rimac, 1,220 m, *Safford in 1887* (NY); *Ball 1882* (GH pro parte, K, NY). Chosica, *Martinet 40* (P, RSA). Huaquicha near Surco, 2,600–2,700 m, *Ferreyra 6067* (US, USM). Surco, 2,000 m, *Asplund 11056* (RSA). Santa Eulalia valley near Huarochiri, *Mc. Hanrish 13, 14* (K). Matucana, *Raimondi in 1877* (USM). Mountains E of Tupe, Atsmito, 3,100 m, *Cerrate 1059* (BM). Canta, 3,000–3,200 m, *Pennell 14603* (F, GH). Cajatambo, 2,740 m, *Sandeman 5322* (K). HUANCAVELICA: Córdoba near Castrovirreina, 3,050–3,300 m, *Metcalf 30288* (G, GH, MO, UC, US).

Cultivated specimens:

Erlangen, Germany, 1795, Herb. *Schreber 159* (M; as *O. capensis*). Erlangen, *in 1800* (M). Botanical Garden of Göttingen, Germany, *in 1803* (LE).

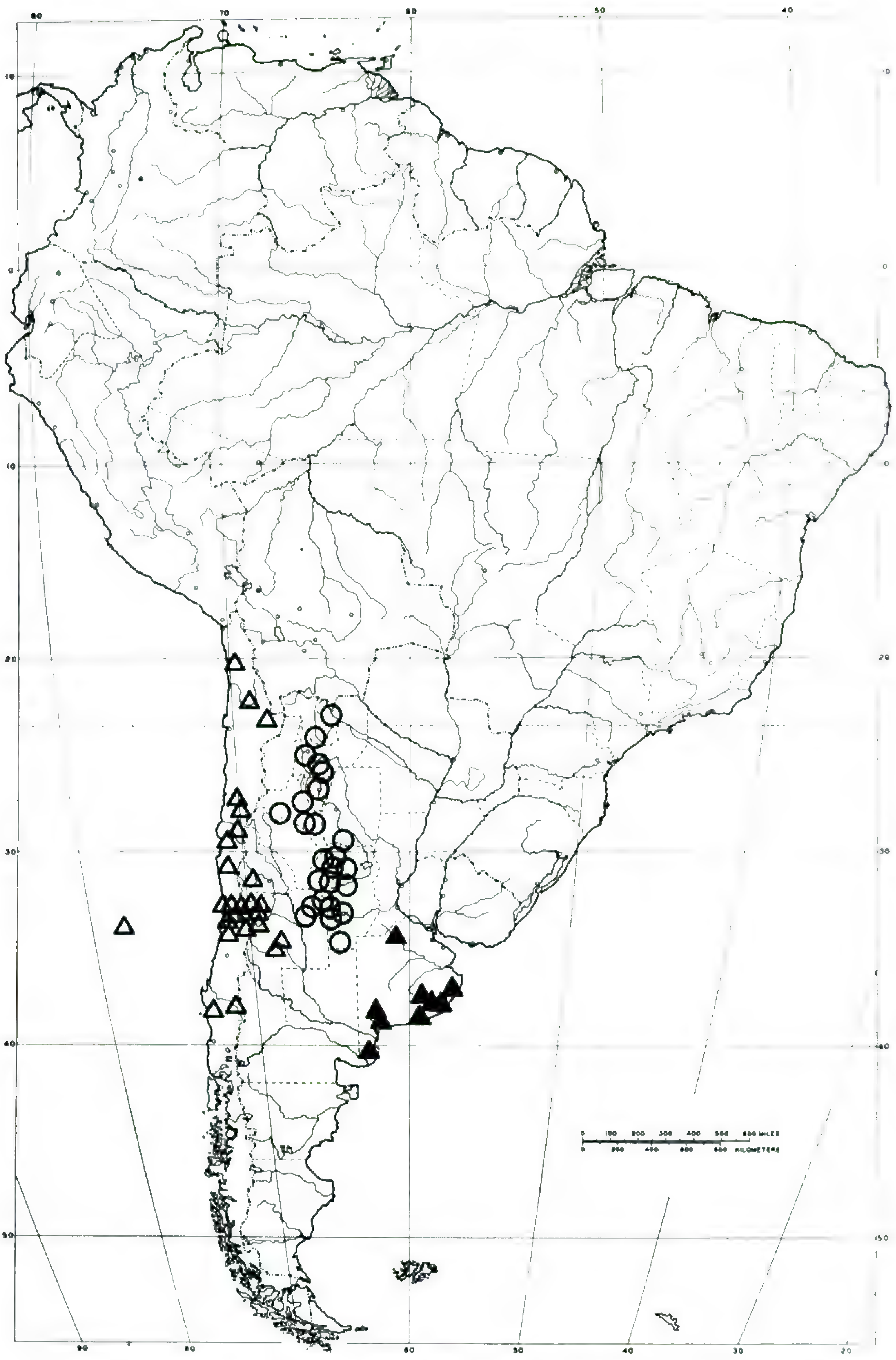


FIGURE 237. Ranges of *Oenothera picensis* subsp. *picensis* (hollow triangles), *O. picensis* subsp. *cordobensis* (circles), and *O. picensis* subsp. *bonariensis* (filled triangles).

The complex heterozygote *O. nocturna* may be separated from the bivalent-forming *O. featherstonei* by its smaller flowers, autogamous breeding system, and usually sinuate leaves. The overwhelming morphological similarity between these species leaves no doubt that *O. featherstonei* contributed one of the chromosomal complexes to *O. nocturna*. The pitting of the seeds in *O. nocturna* (Fig. 190) is very similar to that in *O. laciniata* subsp. *pubescens* (subsect. *Raimannia*). It seems possible that *O. laciniata* subsp. *pubescens* has contributed a genome to *O. nocturna*, and perhaps also to *O. arequipensis* (the other parent being *O. verrucosa*), but these hypotheses have not yet been tested experimentally. Neither *O. nocturna* nor *O. arequipensis* has the nodding buds characteristic of *O. laciniata* subsp. *pubescens*.

Series III. CLELANDIA

Oenothera sect. **Oenothera** subsect. **Munzia** series **Clelandia** Dietrich, ser. nov.

Raimannia sensu Sprague & Riley, Bull. Misc. Infor. 1921: 200. 1921, pro parte.
Oenothera § *Raimannia* sensu Munz & Johnston, Contr. Gray Herb. 75: 16. 1925, pro parte.
Oenothera subgen. *Raimannia* sensu Munz, Physis 11: 279. 1933, pro parte; Amer. J. Bot. 22: 645. 1935, pro parte.

Herbae annuae vel biennes (*O. punae* perennis est), erectae vel prostratae, rosulatae vel erosulatae. Capsula sursum gradatim angustata, specieribus paucis cylindricis, ± erecta, manifeste bractea subtenta connata; valvulae capsulae post dehiscentiam extro curvatae.

Annual or biennial herbs (only *Oenothera punae* perennial), erect or prostrate, forming a rosette or the stem elongating soon after germination, unbranched or with oblique or arching side branches arising from the rosette; plants 2–15(–20) dm tall, or with prostrate branches 5–25 cm long. Stems usually thicker than those of series *Allochroa*, (3–)5–15 mm thick. Plants (1) densely to sparsely strigillose and densely to sparsely long- and short-villous; (2) densely to sparsely strigillose, densely to sparsely long- and short-villous, and moderately to sparsely glandular-pubescent; or (3) densely to sparsely long- and short-villous and densely to sparsely glandular-pubescent. Rosette leaves linear to narrowly oblong, very narrowly elliptic to elliptic or narrowly oblanceolate, gradually narrowed to the petiole or subsessile and narrowly cuneate at the base, 2–25 cm long, 0.1–2.5 cm wide; cauline leaves linear to narrowly oblong, very narrowly elliptic to elliptic or narrowly lanceolate to lanceolate, acute, narrowly cuneate to truncate at the base, sessile or short-petiolate, 1.5–20 cm long, 0.1–2 cm wide; bracts linear, very narrowly elliptic to narrowly elliptic or narrowly lanceolate to narrowly ovate, acute, acute to subcordate at the base, 1.5–6 cm long, 0.1–1.5 cm wide, often with red margins; leaves plane or evidently undulate at the margins, usually irregularly serrate with blunt or sharp teeth. Inflorescence simple or branched; flowers erect or somewhat oblique with respect to the stem. Floral tube 0.5–10 cm long. Buds narrowly oblong to oblong, elliptic to broadly elliptic, or narrowly lanceolate to lanceolate in outline, green to yellowish, often flushed with red, often with red stripes at the junction of the sepals with the floral tube, 0.3–2.5 cm long, 2–6 mm thick. Sepals rarely flecked with dark red; apices of the sepals 0.5–3 mm long, erect

FIGURE 238. Ranges of *Oenothera parodiana* subsp. *parodiana* (hollow triangles), *O. punae* (dots), *O. verrucosa* (filled triangles), and *O. laciniata* subsp. *pubescens* (circles).

or divergent. Petals obovate to very broadly obovate, 0.4–3 cm long, yellow, rarely with an indistinct red spot at the base of each one. Style short, the anthers shedding pollen directly on the stigma at anthesis. Ovary 0.5–2 cm long. Capsule 1.2–4 cm long, 2.5–5 mm thick, in most species gradually narrower upward from a broad base, in a few broadly cylindrical, ± erect, evidently fused with the subtending bract; valves curving outward as in series *Allochroa* when the capsule sheds its seeds. Seeds elliptic to rotund in outline, 0.8–2 mm long, 0.5–0.9 mm thick, light to dark brown, sometimes flecked with dark red-brown spots. Self-pollinating complex heterozygotes. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I; plants with smaller rings very rare).

Type species: *Oenothera elongata* Rusby.

Distribution (Fig. 7): Most species of this series occur at low elevations. Only the species that occur in Bolivia and *O. punae* are characteristic of the high mountains.

This series is dedicated to the late Ralph E. Cleland (1892–1971), student of *Oenothera*. All of the species assigned to it combine one genome derived from series *Renneria* with another derived from series *Allochroa*. See also the remarks on pp. 427 and 434 concerning the relationships of this group.

Many of the species included here are relatively difficult to recognize as members of series *Clelandia* in a pressed condition. The capsules are mostly not cylindrical, however, and they do taper toward the apex. Whereas the capsules of series *Allochroa* always stand out obliquely from the stem, those of series *Clelandia* are more nearly erect, like those of series *Renneria*. In complex heterozygotes that involve *O. affinis*, however—at least in *O. elongata* and *O. pseudoelongata*—the capsules are cylindrical, which might be related to the fact that the capsules in *O. affinis* are somewhat swollen in their upper third. The inflorescence of series *Clelandia* is, as a rule, thicker and more heavyset than that in series *Allochroa*.

35. **Oenothera magellanica** Philippi, Anales Univ. Chile 84: 633. 1893.—Figs. 83, 156.

O. hirsuta Meigen, Bot. Jahrb. Syst. 17: 260, 291. 1893; non (Spach) Steud., Nom. Bot., ed. 2. 2: 206. 1841. LECTOTYPE: Chile, Yerba Loca, 2,000 m, 7 Aug. 1892, *F. Meigen* 539 (SGO, GH photograph).

O. magellanica Philippi var. *chubutensis* Macloskie, Rep. Princeton Univ. Exped. Patagonia 8 (5, 3): 613. 1905. TYPE: not located.

Oenothera stricta sensu Macloskie, Rep. Princeton Univ. Exped. Patagonia 8(5, 3): 614. 1905; sensu Munz, Physis 11: 284. 1933, pro parte; Amer. J. Bot. 22: 661. 1935, pro parte; sensu Bøcher, Dansk Bot. Ark. 22: 90. 1968.

Onothera polymorpha H. Lév. race *odorata* (Jacq.) H. Lév. var. *magellanica* (Philippi) H. Lév., Monogr. Onoth. 363. 1909; Bull. Acad. Int. Géogr. Bot. 19: 323. 1909.

Oenothera mollissima sensu Munz, Physis 11: 282. 1933, pro parte; sensu Bøcher, Dansk. Bot. Ark. 22: 90. 1968.

Oenothera odorata sensu Munz, Physis 11: 284. 1933, pro parte; Amer. J. Bot. 22: 660. 1935, pro parte; Revista Univ. (Santiago) 22: 264. 1937, pro parte.

Erect annual or biennial herb, forming a rosette, unbranched or with a branched main stem and arching or obliquely ascending side branches arising

FIGURE 239. Ranges of *Oenothera parodiana* subsp. *strigulosa* (circles), *O. acuticarpa* (filled triangle), *O. coquimbensis* (hollow triangles), and *O. nocturna* (dots).

from the rosette, 2–12 cm tall. Plants densely to very sparsely strigillose, moderately to sparsely long- and short-villous, rarely sparsely glandular-pubescent. Rosette leaves linear to narrowly oblanceolate, acute, gradually narrowed to the petiole, 10–25 cm long, 0.9–1.5 cm wide; cauline leaves very narrowly elliptic to narrowly lanceolate or narrowly oblanceolate, acute, narrowly cuneate to attenuate at the base, sessile, 5–20 cm long, 0.5–1.2 cm wide; bracts narrowly lanceolate to lanceolate, acute, rounded to truncate at the base, sessile, longer than the capsules they subtend, 4–6 cm long, 0.5–1 cm wide; leaves plane or markedly undulate at the margins, regularly or irregularly serrate, the teeth blunt or sharp. Inflorescence simple or branched. Floral tube 1.3–2.5(–3) cm long. Buds oblong to lanceolate in outline, green to yellowish green, often flushed with red, 1–2 cm long, 4–5 mm thick; apices of the sepals 1–2 mm long, erect or divergent. Petals very broadlly obovate, 1.5–2.5 cm long. Anthers 6–8 mm long. Filaments 9–12 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.5–4.5 cm long. Stigma lobes 3–5 mm long. Ovary 1.5–2 cm long. Capsule 2.5–4 cm long, 3–5 mm thick. Seeds elliptic in outline, 1.4–2 mm long, 0.6–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14*, ring of 12 and 1 bivalent**, ring of 8 and ring of 6*** or ring of 10 and 2 bivalents**** at meiotic metaphase I). Flowering time: Northern area, November–April; southern area, November–March.

Lectotype: Argentina, Prov. Santa Cruz, Río near Lago Argentino (Lago Santa Cruz), 15 Feb. 1879, *E. Ibar* (*2187*) (SGO-041392, GH photograph).

Distribution (Fig. 232): Most frequent along the western foothills of the Andes in the provinces of San Juan, Mendoza, Neuquén, Río Negro, Chubut, and Santa Cruz in Argentina, but with isolated stations in the provinces of Aconcagua, Santiago, Aisén, and Magellanes in Chile, and very widely scattered localities in the provinces of Córdoba, San Luis, and Buenos Aires (Bahía Blanca), Argentina.

Specimens examined from cultivated plants:

ARGENTINA. SAN JUAN: Dep. Iglesias, Tocota, 2,480 m, *Ruizthal in 1962** (DUSS, MO). MENDOZA: Stony slopes at Ruta 7, 1 km of Punta de Vacas, 2,500 m, *Santarius 1459**, *1461*, *1464*, *1467**, *1475* (DUSS; *1459*, *1467* also M; *1467* also MO). Dry rivulet bed near Ruta 7, 4.5 km E of Punta de Vacas, 2,450 m, *Santarius 1476**, *1480*, *1483*, *1485*, *1489**, *1490*, *1492**, *1496* (DUSS; *1480*, *1489* also CTES, M, MO). Stony slope along Ruta 7, 1 km W of Polvaredas, 2,450 m, *Santarius 1504**, *1506*, *1513**, *1518* (DUSS; *1504* also MO). Arroyo Polvaredas E of Polvaredas, 2,400 m, *Santarius 1523**, *1525*, *1526**, *1528**, *1532*, *1534*, *1536*, *1540*, *1541**, *1544*, *1548** (DUSS; *1526*, *1528*, *1541*, *1544*, *1548* also CTES, M, MO). Waste and stony places ca. 2 km N of Tupungato 1,250 m, *Santarius 1562** (DUSS). Rocks and stony slopes of the Precordillera near Villavicencio, 12 km above Villavicencio on Ruta 7, 2,600 m, *Santarius 1577**, *1578*, *1579**, *1580* (DUSS; *1579* also CTES, M, MO). 10.5 km above Villavicencio, 2,500 m, *Santarius 1581**, *1582*, *1584**, *1588**, *1589**, *1591**, *1592*, *1593**, *1595* (DUSS; *1581*, *1584*, *1588*, *1591*, *1592*, *1593*, also CTES, M, MO). 9.5 km above Villavicencio at km 1160, 2,350 m, *Santarius 1597**, *1598*, *1599**, *1602**, *1603**, *1607*, *1608* (DUSS; *1598*, *1599*, *1602* also CTES, M; *1598*, *1599*, *1602*, *1607* also MO). 9 km above Villavicencio, 2,300 m, *Santarius 1610**, *1616*, *1621**, *1622**, *1625** (DUSS; *1621*, *1622*, *1625* also CTES, M, MO). 5 km above Villavicencio (Los Surtidores), 2,050 m, *Santarius 1638*****, *1639*, *1641*, *1642*, *1643**, *1646**, *1649* (DUSS; *1646* also M, MO). Villavicencio, 1,700 m, *Santarius 1652**, *1653*, *1654* (DUSS; *1653* also CTES, M, MO). Uspallata, *Hecht 1964–79** (DUSS). NEUQUÉN: Stony places at Río Limay, 6 km E of Piedra del Águila, *Santarius 607**, *609** (DUSS, M, MO; *607* also CTES). Stony places near the ferry across Río Limay at Ruta 237, ca. 75

km SSW of Piedra del Águila, *Santarius 645** (CTES, DUSS, M, MO, SP). RÍO NEGRO: San Carlos de Bariloche, *Stubbe in 1961** (CTES, DUSS, M, MO). Sandy and stony waste places at the shore of the Lago Nahuel Huapí, near railroad station of Bariloche, 780 m, *Santarius 646*, 647, 649*, 652, 655, 656*, 657, 659, 661, 663*, 668*, 674, 676, 677, 692, 694, 700, 706*, 709, 734, 736, 744, 751* (DUSS; *649, 657, 668, 677, 706* also CTES; *646, 649, 657, 668, 677, 706* also M; *646, 649, 657, 668, 676, 677, 706* also MO). N slope of Cerro Otto, ca. 3 km W of Bariloche, along road to the top on volcanic ashes, 850 m, *Santarius 784*, 786, 789*, 796, 797* (DUSS; *784, 789* also CTES, M, MO). El Bolsón, 325 m, *Santarius 838, 840*, 842, 847, 851* (DUSS; *840* also CTES, MO). NW slope at km 17.5 of the road from Bariloche to Villa Catedral, 1.5 km N of Villa Catedral, 900 m, *Santarius 853** (DUSS, MO). CHUBUT: Meadows about 11.5 km SSW of El Bolsón on the road to Lago Puelo, 300 m, *Santarius 821** (DUSS). Airport of Esquel, 675 m, *Santarius 903*, 904, 905, 907*, 910, 912* (DUSS; *903, 907* also CTES, M, MO); ibid., *Santarius 1393*, 1394, 1398*, 1404* (DUSS; *1393* also M, MO). SANTA CRUZ: Dry rivulet bed 2 km N of bridge on Ruta 3 across Río Gallegos, *Santarius 997** (DUSS). Dep. Lago Argentino, Parque Nacional Los Glaciares, N slopes near Guardabosque about 48 km WSW of Calafate, 200 m, *Santarius 1067*, 1070, 1074–1076, 1081*, 1086*, 1088, 1089*, 1090–1092* (DUSS; *1086* also M; *1081, 1086* also MO). Above the campgrounds ca. 51 km WSW of Calafate, 250 m, *Santarius 1095*, 1102, 1104, 1108, 1111, 1116, 1121, 1122, 1126* (DUSS; *1104* also MO). Road ca. 1 km S of Punta Bandera near Lago Argentino, 200 m, *Santarius 1128*, 1130* (DUSS). Road to Punta Bandera near fork to Ventisquero Moreno, 250 m, *Santarius 1133*, 1135, 1138, 1147*, 1148, 1150, 1159* (DUSS; *1133* also MO). Stony and sandy places near Perito Moreno, 380 m, *Santarius 1254*, 1255, 1260, 1268*, 1269, 1270**, ** (DUSS; *1254* also MO). 4 km W of Estancia Las Chilcas, ca. 46 km W of Perito Moreno, 250 m, *Santarius 1338*, 1339, 1344, 1345* (DUSS). Río Los Antiguos W of Los Antiguos, 220 m, *Santarius 1303*, 1304–1306, 1309, 1311, 1315*, 1316*, 1317, 1320*, 1321, 1322, 1323** (DUSS; *1306* also CTES; *1303, 1306, 1316* also M; *1303, 1306, 1320, 1322* also MO).

CHILE. AISÉN: Puerto Ibáñez at Lago Buenos Aires, on stony places on the sea shore and slopes up to 300 m above lake, *Nodt in 1961* (DUSS). Waste places, shore of Lago Buenos Aires in Chile Chico, 210 m, *Santarius 1286*, 1287, 1290, 1292, 1295****, 1298**** (DUSS; *1286* also M, MO). MAGELLANES: Road 0–4 km E of Puente Lago Amarga, W of Lago Sarmiento and S of Lago Nordenskjold, 150 m, *Santarius 998*, 1001*, 1004*, 1007, 1011, 1014, 1023*, 1024, 1025*, 1028, 1036, 1037, 1041* (DUSS; *998, 1001, 1023, 1025* also M; *998, 1001, 1004* also MO).

Representative specimens examined:

ARGENTINA. SAN JUAN: Bajada de Cuesta Vieja, *Hossens 2578* (CORD). Valley of Río de Los Chupadores, *Hossens 2537* (CORD). Leoncito, *Schegaray in 1876* (CORD). Dep. Sarmiento, El Federal, *Cuezzo 1705* (LIL, RSA). Arroyo los Dos Puentes near Iglesias, *Spegazzini 231* (BAB). Road from Portezuelo to Agua Negra, 3,100 m, *Fabris et al. 8383* (LP, SI). MENDOZA: Villavicencio, 2,900 m, *Boelcke 9955* (BAA, BAB); *Bartlett 19424* (GH, MICH, UC, US); *O'Donell 1019* (LIL); *Roig 5305* (CORD); *Sparre 1498* (S); *Nicora 4334* (SI). Puente del Inca, *Kurtz 3504* (CORD). Punta de Vacas, *Haumann in 1918* (BA). Las Heras, Quebrada del Toro, *Lourteig 816* (LIL, NY). Dep. Luján, Est. El Salto, 2,950 m, *Ruiz Leal 6183* (Leal). Dep. Malalhue, Los Molles, 1,850–1,950 m, *Ruiz Leal 20887* (Leal). Tupungato, *Ruiz Leal 2784a* (Leal, POM). San Rafael, Minacar at Río Grande, 2,500 m, *Lourteig 734* (LIL). Cerro Diamante, *Gillies* (K). Cerro Nevado, *Ruiz Leal 2506* (Leal, POM). Arroyo Mangas in valley of Río Atuel, 1,900 m, *Wilczek 411* (G, US, Z). Banks of Río Atuel near El Sosneado, *Burkart et al. in 1942* (SI). Refugio Gral, Alvarado near San Carlos, *Cuezzo & Barkley 20Mz475* (LIL). Campo de los Andes near Tunuyan, 1,800 m, *Araque 1126* (LIL). Gral. Gutierrez near Maipú, *Ruiz Leal 25-2108* (POM). NEUQUÉN: Traful, *Cabrera & Job 397* (LP, NY). Est. La Primavera, *Castellanos in 1938* (RSA). Between Pulmari and China Muerta, *Maldonado 669* (F). Between Ñorquin and Codihue, *Kurtz 6287* (CORD). Las Lajas, *Spegazzini 100* (BAB). Lago Nonthué, between Puerto de Gendarmeria and Arroyo near Hua Hum, *Valla 3286* (BAA). Paso Flores at Río Limay, *in 1938* (LIL-80006). Aluminé, *Giacobbi 12935* (BAA, POM). Santa María at Lago Nahuel Huapí, *Ljunguer in 1934* (NY). RÍO NEGRO: San Carlos de Bariloche, *Lesse 19* (P); *Buchtien 1356* (BREM pro parte, GH pro parte); *Meyer 7543* (LIL, NY). Cerro Otto, *De Barba 945* (LIL, RSA); *Boelcke 1702* (CTES). Arroyo Ñireco near Bariloche, *Meyer 8060* (LIL). Laguna Cari Lauquén, *Kurtz 6110* (CORD). El Bolsón, *De Barba 422* (F, LIL). Perito Moreno, *Novatti 10* (LP). Gral. Conesa, *Meyer 7119* (LIL). Choele Choel, 152 m, *O'Donell 795* (LIL). CHUBUT:

Between El Bolsón and Colonia 16 de Febrero, *Illin 237* (BR, CORD, HBG, SI). Tehuelches, between Gob. Costa and José de San Martín, *Moreau 3619* (BAB). Valley of Río Chubut, *Koslowsky 31-1643* (POM). Est. Leleque near Cushamen, *Meyer 7776* (GH, LIL). Río Percey, *Kühnemann 648* (RSA). Cordillera, Río Corcovado, *Illin 40* (UC). Dep. Escalante, Est. Los Manantiales near Cañadón Pilar, 380 m, *Eyerdam et al. 23800* (G, GH, MO, S, UC). Lago Epuyén, *Soriano 1365* (BAA). Esquel, *Garcés 286* (SI). SANTA CRUZ: Río Gallegos, *Tauber 89* (BR). Cañadón León, *Cittadini 20* (BAB). Puerto Deseado, *Correa 3300* (BAA, BAB, MO). Güer Aike, *O'Donell 4070* (LIL, RSA). Lago Viedma, 300 m, *Donat in 1932* (POM). Río Oro, *Donat 335* (SI). Lago Posadas, 200 m, *Donat 256* (BM, F, G, GH, HBG, K, LIL, MO, NY, S, SI, UC, Z). Junction of Río Blanco and Río Electrico, 720 m, *Luti 3726* (CORD). Calafate at Lago Argentino, *Hicken & Haumann 607* (SI). Between Lago Argentino and Lago Viedma, *Eyerdam et al. 24347* (GH, K, UC). Lago Buenos Aires, *Skottsberg 657* (S). CÓRDOBA: El Durazno near Punilla, *Meyer & Sleumer 15669* (LIL). Pampa de Achala, *Meyer & Sleumer 15533* (LIL). Copina, *Burkart 7326* (LIL). Valle de los Reartes, *Castellanos in 1920* (LIL). Quebrada del Tigre near San Javier, *Bridarolli 1582* (LP). SAN LUIS: Sierra de Comechingones, El Rincón, *Hunziker 11828* (CORD). El Morro, 1,100 m, *Hunziker 12596* (CORD); *Pastore in 1913* (SI-4671). El Rincón, *Conrad & Dietrich 144, 146, 148, 150, 153* (DUSS). BUENOS AIRES: Bahía Blanca, *Claraz 218* (G).

CHILE. ACONCAGUA: Juncal, 2,200 m, *Buchtien in 1903* (BM, BREM, GH, L, LY, M, S, SI, US, W). Road to Argentina, at Río Blanco, *Nicora 4397* (SI). SANTIAGO: Río Yeso near Romeral, *Biese in 1944* (LIL). San Gabriel, 1,500 m, *Montes 527* (K, MO). AISÉN: Valle Coihaique, *Rentzell 6129* pro parte (GH). Est. El Paine, *Paschke 12246* (CONC). Salto Grande del Paine, *Pisano 2342* (CONC). Mina Silva at Lago Buenos Aires, *Heim in 1939* (Z). Chile Chico at L.B.A., *Pfister 18480* (CONC). Valle Ibáñez, *Belem 22799* (CONC). Aisén, *Dusén in 1897* (CORD), *486* (S). MAGELLANES: Lago Sarmiento near Puerto Natales, *Rüe in 1958* (P). Ultima Esperanza, *Magens in 1954* (CONC). Laguna Mantecón near Punta Arenas, *Cekalovic in 1950* (CONC). Isla Grande I, *Gusinde 189* (W).

Specimen from plants cultivated in garden:

Botanical Garden Kew, England, *in 1873* (K; as *O. biennis* var. *undulata*).

This species derives its genomes from *O. santarii* and *O. odorata*. Experimental hybridization with these species has established the origin of *O. magellanica* beyond any doubt. Together with *O. odorata*, *O. magellanica* is the most frequent species of this section in southern South America, and the two often grow together. It can be distinguished from *O. odorata* by an array of the characteristics it has obtained from *O. santarii*: upright habit, heavier stems, smaller flowers. From *O. santarii* it can easily be distinguished by its longer fruits.

On the basis of a general similarity in habit, *O. magellanica* has often been confused with *O. stricta*, but of course that complex heterozygote has derived both of its genomes within series *Allochroa*. The short bracts of *O. stricta*, ultimately derived from *O. ravenii*, immediately separate it from *O. magellanica*.

The pattern of variation in *O. magellanica* suggests that backcrossing with *O. santarii* and *O. odorata*, with the consequent introduction of genetic material into *O. magellanica*, has been fairly frequent. Within *O. magellanica*, however, plants with anything except a complete ring of 14 chromosomes are very rare, suggesting a very high level of selection for the restoration of complex heterozygosity following hybridization. Where the range of *O. magellanica* overlaps that of *O. santarii*, the variation pattern of the former converges on that of the latter, and it begins to resemble series *Renneria* in general. The farther south one goes, however, the stronger the influence of *O. odorata* on the populations of *O. magellanica*. This influence is expressed strongly in the capsules, which become longer and more similar to those of *O. odorata* southward. The process does not go so far, however, that the boundary between the two is blurred; *O. magella-*

FIGURE 240. Range of *Oenothera siambonensis* (dots).

nica can always be separated easily from *O. odorata* because of its more compact inflorescence and sturdier habit. Some herbarium specimens are difficult to determine if they include insufficient or immature material; but in living plants, especially under uniform conditions of cultivation, there is never any doubt.

36. **Oenothera villaricae** Dietrich, sp. nov.—Figs. 4, 88, 157, 205.

O. berteriana "Erlangen" Haustein, Z. Indukt. Abstammungs- Vererbungsl. 84: 418. 1952; Cleland, Jap. J. Genet. 43: 332. 1968.

Herba annua vel biennis, erecta, rosulata, simplex vel caulis principalis ramosus et ramis arcuate vel oblique e rosula ascendentibus, 5–10(–15) dm alta. Plantae densissime vel sparse strigulosae et moderate vel sparse villosae. Folia rosulae anguste elliptica vel oblanceolata, acuta, lamina in petiolum brevem gradatim decrescens vel subsessili, 10–20 cm longa, 1–2 cm lata; folia caulina anguste elliptica vel anguste lanceolata, acuta, basi acuta vel truncata, sessilia, 8–15 cm longa, 1–2 cm lata; bractea lanceolata vel anguste ovata, acuta, basi truncata, sessilia, praecipue superiora rubro-marginata apiceque incurvata, quam capsula subtena breviora vel ad eas subaequalia, raro longiora, 2–4(–6) cm longa, 0.8–1.5 cm lata; folia plerumque marginibus exigue undulatas, irregulariter obtuseque serrata. Inflorescentia plerumque simplex. Tubus floralis 2–3 cm longus. Gemmae ambito oblongae vel lanceolatae, virides vel flavovirentes, saepe rubrae, plerumque junctura sepalorum tubo florali anguste rubro-fasciatae; apices sepalorum 2–3 mm longi, erecti vel divergentes. Petala latissime obovata, interdum basi pallide rubro-maculata, 1.5–2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.3–2 cm longum. Capsula 2–3 cm longa, 3–4 mm crassa. Semina ambito late elliptica, 1.1–1.5 mm longa, 0.5–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual or biennial herb, forming a rosette, unbranched or with a branched main stem and arcuate or obliquely ascending side branches from the rosette, 5–10(–15) dm tall. Plants very thickly to sparsely strigillose and moderately to sparsely villous. Rosette leaves narrowly elliptic to oblanceolate, acute, gradually narrowed to the short petiole or subsessile, 10–20 cm long, 1–2 cm wide; cauline leaves narrowly elliptic to narrowly lanceolate, acute, acute to truncate at the base, sessile, 8–15 cm long, 1–2 cm wide; bracts lanceolate to narrowly ovate, acute, truncate at the base, sessile, especially the upper ones with red margins and an incurved tip, shorter than the capsules they subtend or subequal to them, rarely longer, 2–4(–6) cm long, 0.8–1.5 cm wide; leaves mostly weakly undulate at the margins, irregularly serrate with blunt teeth. Inflorescence usually unbranched. Floral tube 2–3 cm long. Buds oblong to lanceolate in outline, 1.2–1.8 cm long, 4–6 mm wide, green or yellowish green, often flushed with red, usually red striped at the junction of the sepals with the floral tube; apices of the sepals 2–3 mm long, erect or divergent. Petals very broadly obovate, sometimes with a weak basal red spot on each one, 1.5–2 cm long. Anthers 6–7 mm long. Filaments 7–11 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 3–4.5 cm long. Stigma lobes 3–4 mm long. Ovary 1.3–2 cm long. Capsule 2–3 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, 1.1–1.5 mm long, 0.5–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–March.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 2 Aug. 1972. Source: Chile, Prov. Cautín, Molco at Lago Villarica, end of 1960, *W. Stubbe* (MO-2155226, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 234): In the Chilean provinces of Cautín, Valdívia, Osorno, Llanquihue, and on Isla Chiloe, as well as in a few localities on the eastern slope of the Andes in the Argentine provinces of Neuquén, Río Negro, and Chubut.

Specimens examined from cultivated plants:

CHILE. CAUTÍN: Sitio Göpfert at Lago Villarica, meadow above the seashore between Antumalal and Pucón, *Göpel in 1961** (CTES, DUSS, M, MO). Laguna Verde at Río Allipén near Volcán Llaima, *Göpel in 1961** (CTES, DUSS, M, MO). Molco at Lago Villarica, *Stubbe in 1960** (DUSS, M, MO). VALDIVIA: Taco Tres at Río San Pedro near Lago Rinihue, *Stubbe in 1961** (CTES, DUSS, M, MO). Las Ánimas near Valdivia, *Göpel in 1961** (CTES, DUSS, M, MO). Isla Teja in Valdivia, *Stubbe in 1960** (CTES, DUSS, M, MO). Collico near Valdivia, *Koch in 1960** (DUSS). Along the railroad near Antilhue, *Stubbe in 1961** (CTES, DUSS, M, MO). OSORNO: Stony places at S edge of Osorno, *Stubbe in 1961** (CTES, DUSS, M, MO). Pan-Amer. Highway, 5 km S Valdivia-Osorno boundary, *Wiens in 1967** (CTES, DUSS, MO).

ARGENTINA. NEUQUÉN: Pucara in the Parque Nacional Lanín, *Schachovsky in 1965** (DUSS). CHUBUT: Meadows ca. 11.5 km SSW of El Bolsón along road to Lago Puelo, 300 m, *Santarius 823**, *824*, *825**, *831**, *833* (DUSS; *823* also CTES, M; *823*, *833* also MO).

CULTIVATED: *O. "berteriana"* from the Botanical Garden of Erlangen in Germany, received in 1960* (CTES, DUSS, M, MO).

Additional specimens examined:

CHILE. CAUTÍN: *Calvert in 1914* (BM). Freire, *Claude-Joseph 5899* (US). Río Zuapa, *Bullock in 1905* (G). VALDIVIA: Valdivia, *Lechler* (M); *Hollermeyer 56* (S); *Buchtien in 1903* (US), *in 1898* (US); *Gay 81* (P). Railroad to Hueyelhue, *Buchtien in 1904* (M, P). Panguipulli, *Gay in 1834* (G, SGO). OSORNO: Lago Llanquihue, *Calvert in 1912* (BM). CHILOE: Canal de Dalcahue, *Funck 126* (P). Without exact locality: *Niemeyer 91* (HBG).

ARGENTINA. NEUQUÉN: Lago Quillén, *Dawson & Schwabe 2874* (BAB). RÍO NEGRO: Bariloche, *Fabris 1124* (M). El Bolsón, *Meyer 7884* pro parte (NY); *Illin 6875* (BAB).

Specimen from plants cultivated in garden:

Botanical Garden of Valence, Italy, from seeds of the Botanical Garden at Rome under the name *O. berteriana* Spach, plant of Chile, 1923, Herb. *E. J. Neyraut 14-140* (MPU). This specimen is identical with the strain known to geneticists as *O. berteriana*. Another specimen was seen from the Botanical Garden Bremen, Germany, *Fahrenholtz in 1923* (BREM).

This newly proposed species has been known to geneticists for some time, since it is identical with the "Erlangen" strain said to be *O. berteriana*. The original provenance of this line is unknown, but presumably it came from one of the provinces of Chile named above. *Oenothera berteriana* itself is a synonym of *O. affinis*.

Like *O. magellanica*, most herbarium specimens of *O. villaricae* are identified as *O. stricta*, which of course had a different origin. The *Renneria* genome of *O. villaricae* was once more contributed by *O. santarii*, whereas its *Allochroa* genome is derived from *O. ravenii* (see also Cleland, 1968). Since, as has been pointed out several times, Chile has no native chromosomally homozygous species of the subsection (except for *O. coquimbensis*), and since the main area of *O. villaricae* seems rather clearly to be Chilean, it probably originated following hybridization between *O. magellanica* and *O. stricta*.

The F_1 hybrids between *O. santarii* and *O. villaricae* consist of two classes, one like each parent. Hybridization with *O. ravenii* is only possible if that species is used as the male parent; the plastids of chromosomally homozygous *O. ravenii* from Brazil do not function in a genetic background of *O. villaricae*.

FIGURE 241. Range of homozygous *Oenothera santarii* (filled triangles) and as a chromosomal complex in *O. magellanica* and *O. villaricae* (circles).

They are colorless, and hybrids between these two species are viable only when there are sufficient green plastids derived from the *O. villaricae* parent. This is usually only the case when *O. villaricae* is the female in the hybridizations.

One of the classes of F_1 hybrids between *O. villaricae* and *O. ravenii* is identical to *O. ravenii*, but the second class does not exactly match *O. villaricae*. This is probably because the large flower size of *O. ravenii* is dominant in *O. villaricae*, and also because the *O. ravenii* complex in *O. villaricae* is derived via *O. stricta* and probably considerably altered in the course of evolution of that species.

Oenothera villaricae can be distinguished from *O. magellanica* by its shorter, red-margined bracts and shorter capsules. Both species differ from *O. stricta* in their upright, sturdy habit and more compact inflorescence.

The Argentinan plants of *O. villaricae* are somewhat different from the Chilean ones in that their bracts are usually shorter. This would seem to indicate a stronger influence of the *O. ravenii* genome. In addition, they have a somewhat more delicate habit and are consistently taller when grown under uniform cultural conditions. It does not seem desirable to separate them taxonomically, however, because they have had a common origin and are closely related. If all of the small differences within the section that are preserved by the syndrome of self-pollination and complex heterozygosity, and which have in many cases come to characterize populations, were to be recognized taxonomically, one could recognize literally hundreds of species without any gain whatsoever in taxonomic utility. Taxonomy serves its end better as a device for summarizing and grouping information about a particular group of organisms, not by splitting them into an excessive number of categories.

37. **Oenothera hechtii** Dietrich, sp. nov.—FIGS. 89–91, 158.

O. parodiana "Villa Nougues" Hecht, Indiana Univ. Publ. Sci. Ser. 16: 277. 1950; J. Hered. 61: 199. 1970.

Herba annua vel biennis, erecta, rosulata, simplex vel caulis principalis parce ramosus et ramis late arcuato e rosula ascendentibus, 5–10 dm alta. Plantae parce vel sparse strigulosae et villosae, circum inflorescentiam densiore. Folia rosulae angustissime elliptica, acuta, basi acuta, sessilia, 12–16 cm longa, 2–2.5 cm lata; folia caulina anguste oblonga vel anguste elliptica, acuta, basi acuta vel rotundata, sessilia, 6–12 cm longa, 1–2 cm lata; bractea lanceolata, acuta, basi rotundata vel truncata, sessilia, 2.5–3 cm longa, 0.8–1.2 cm lata; folia plana, irregulariter serrulata. Inflorescentia simplex. Tubus floralis 4–5.5 cm longus. Gemmae ambito lanceolatae, flavo-virentes, junctura sepalorum tubo florali rubro-fasciatae, 1.5–1.8 cm longae, 4–6 mm crassae; apices sepalorum ca. 1.5 mm longi, erecti. Petala obovata, 1.8–2.2 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1–1.3 cm longum. Capsula 2.5–3 cm longa, ca. 3 mm crassa, extremi valvarum distincti, discreti, crenatique. Semina ambito late elliptica, 0.9–1.1 mm longa, 0.6–0.7 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual or biennial herb, forming a rosette, with simple or little-branched main stem and widely arching side branches arising from the rosette, 5–10 dm tall. Plant moderately to sparsely strigillose and villous, more densely so in the region of the inflorescence. Rosette leaves very narrowly elliptic, acute, attenuate at the base, sessile, 12–16 cm long, 2–2.5 cm wide; cauline leaves narrowly oblong to narrowly elliptic, acute, acute to rounded at the base, ses-

sile, 6–12 cm long, 1–2 cm wide; bracts lanceolate, acute, rounded to truncate at the base, sessile, 2.5–3 cm long, 0.8–1.2 cm wide; leaves plane at the margins, irregularly serrulate. Inflorescence unbranched. Floral tube 4–5.5 cm long. Buds lanceolate in outline, yellowish green, red striped at the junction of the sepals with the floral tube, 1.5–1.8 cm long, 4–6 cm thick; apices of the sepals ca. 1.5 mm long, erect. Petals obovate to broadly obovate, 1.8–2.2 cm long. Anthers 5–6 mm long. Filaments 10–13 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 5–7 cm long. Stigma lobes 4–5 mm long. Ovary 1–1.3 cm long. Capsule 2.5–3 cm long, ca. 3 mm thick, with distinct, free, crenate ends to the valves. Seeds broadly elliptic in outline, 0.9–1.1 mm long, 0.6–0.7 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Argentina, Prov. Tucumán, Villa Nougés near Tucumán, *A. Hecht 1964-81* (MO-2155202, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 235): So far known only from the type locality.

Specimen examined from cultivated plants:

ARGENTINA. Prov. *Tucumán*, Villa Nougés near Tucumán, *Hecht 1964-81** (DUSS, M, MO).

This new species is dedicated to Adolph Hecht (1914–), student of *Oenothera*. Because of its superficial similarity to *O. parodiana* subsp. *brasiliensis*, it was not realized at first that *O. hechtii* belonged to series *Clelandia*. Consequently it has not yet been possible to test its parentage by experimental hybridization, although some deductions can be made on a morphological basis. Clearly, the *Allochroa* element in *O. hechtii* can have been derived only from *O. ravenii*. The rosettes of *O. hechtii* and its flowers, which have relatively long tubes and sometimes overtop the stem, are reminiscent of those of *O. longituba* of series *Renneria*.

38. **Oenothera elongata** Rusby, Mem. Torrey Bot. Club 3(3): 33. 1893.—FIGS. 159, 183.

O. serratifolia Krause, Repert. Spec. Nov. Regni Veg. 1: 168. 1905. TYPE: Bolivia, Dep. Tarija, Toldos near Bermejo, in a canyon, ca. 2,000 m, 9 Dec. 1903, *K. Fiebrig 2374* (B, destroyed in World War II, UC 292 and 689 fragments and photograph, F, GH and POM photographs; G, isotype).

Erect annual herb, not forming a rosette, unbranched or branched from the base upward, 6–15 dm tall. Plants densely to sparsely strigillose, densely to sparsely long- and short-villous, and densely to sparsely glandular-pubescent. Cauline leaves very narrowly elliptic to lanceolate, acute, attenuate to rounded at the base, 5–12 cm long, 0.5–1.5 cm wide; bracts lanceolate to narrowly ovate, acute, 2.5–5 cm long, 1–1.5 cm wide, longer than the capsules they subtend; leaves plane at the margins and remotely serrate, the teeth blunt. Inflorescence simple or branched. Floral tube 7–10 cm long. Buds narrowly oblong to lanceolate in outline, 1.5–2.5 cm long, 4–6 mm thick, often red striped at the junction

FIGURE 242. Range of homozygous *Oenothera odorata* (dots) and as a chromosomal complex in *O. grisea*, *O. magellanica*, *O. parodiana* subsp. *parodiana*, *O. picensis*, *O. rivadaviae*, and *O. stricta* (hollow triangles).

of the sepals with the floral tube and often flushed with red elsewhere; apices of the sepals 1.5–3 mm long, erect or divergent. Petals very broadly obovate, 1.5–3 cm long. Anthers 7–10 mm long. Filaments 15–24 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 8–12.5 cm long. Stigma lobes 5–7 mm long. Ovary 1.2–1.5 cm long. Capsule 2–3 cm long, 4–5 mm thick. Seeds elliptic to broadly elliptic in outline, 1.1–1.5 mm long, 0.6–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–April.

Type: Bolivia, Dep. La Paz, vicinity of La Paz, 3,280 m, 1889, *A. M. Bang 54* (NY, holotype; BM, G, GH, K, LE, MICH, MO, NY, US, W, isotypes).

Distribution (Fig. 236): Elevations of 1,200 to 3,800 m in the Bolivian Andes, in the departments of La Paz, Cochabamba, Chuquisaca, and Tarija; also an isolated station in the province of Catamarca, Argentina. See p. 439.

Specimens examined from cultivated plants:

BOLIVIA. LA PAZ: Slope on the east side of Valle de Irpavi, about 0.5–1 km N of Calacoto (SE of La Paz), above the military terrain along an irrigation ditch, 3,450 m, *Santarius 2026**, *2027*, *2028*, *2029*, *2030**, *2031–2033* (DUSS; *2026* also M; *2026*, *2028* also MO). TARIJA: Rocks and stony places along the road from Villazón to Tarija, at km 27, 2,700 m, *Santarius 1956** (DUSS); at km 26, 2,650 m, *Santarius 1957** (CTES, DUSS, M, MO); at km 25, above Tucumilla, 2,600 m, *Santarius 1958*, *1959** (DUSS; *1959* also CTES, M, MO).

ARGENTINA. CATAMARCA: La Banderita, on the road from Andalgala to Concepción (border of Prov. Tucumán), 1,800 m, *Diers in 1959** (CTES, DUSS, M, MO).

Additional specimens examined:

BOLIVIA. LA PAZ: La Paz, 3,550 m, *Buchtien 39* pro parte (C, L, LIL, M), *77* (BM, C, F, G, GH, K pro parte, LD, LIL, MO, NY, POM, SI, Z). Obrajes, 3,500 m, *Buchtien in 1907* (SI-4753); *Häberli in 1929* (Z). Prov. Larecaja, Sorata near Colani, 2,900 m, *Mandon 629* (BM, G, K, P, W). Muñecas near Charazani, 2,700 m, *Cardenas 3833* (POM). COCHABAMBA: Prov. Chaparé, 32 km NE of Cochabamba, 1,200 m, *Eyerdam 24996* (G, UC pro parte). Choro, above the Cocapata River about 100 mi NW of Cochabamba across the Tunari range, 3,050 m, *Brooke 6922* (BM, F, NY). CHUQUISACA: Prov. Tomina, *Weddell 3704 in 1845–1846* (P).

Oenothera elongata has derived one chromosomal complex from *O. longituba*, the second from *O. affinis*. This combination might have originated in southern Bolivia, either through hybridization of the chromosomally homozygous parental species, or by the transmission of a *longituba*-complex through *O. tarijensis* or *O. recurva*, these hybridizing with *O. affinis*. See also the remarks on complex heterozygosity on p. 440.

39. **Oenothera pseudoelongata** Dietrich, sp. nov.—FIG. 160.

Herba annua, erecta, erosulata, simplex vel e basi sursum ramosa, 5–8 dm alta. Plantae dense strigulosae, dense pilis longis brevibusque villosis praeditae, et circum inflorescentiam glanduloso-pubescentes. Folia caulina angustissime elliptica vel lanceolata, acuta, basi acuta vel rotundata, 5–10 cm longa, 0.7–1 cm lata; bractea lanceolata vel anguste ovata, acuta, basi truncata, 2.5–3 cm longa, 0.8–1 cm lata, quam capsula subtenta longiora; folia plana, remote obtuseque vel acute serrata. Inflorescentia simplex vel ramosa. Tubus floralis 5–6 cm longus. Gemmae ambito anguste oblongae vel lanceolatae, 0.8–1.1 cm longae, 3.5–4 mm crassae, saepe rubrae, junctura sepalorum tubo florali rubro-fasciatae; apices sepalorum 2–3 mm longi, erecti vel divergentes. Petala latissime obovata, quam stamina breviora, 0.8–1.3 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 0.9–1.1 cm longum. Capsula 1.5–2.5(–3) cm longa, 3–4 mm crassa. Semina ambito elliptica, 1.5–1.8 mm longa, 0.7–0.8 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, simple or branched from the base upward, 5–8 dm tall. Plants densely strigillose, densely long- and short-villous, and also glandular-pubescent in the region of the inflorescence. Cauline leaves very narrowly elliptic to lanceolate, acute, acute to rounded at the base, 5–10 cm long, 0.7–1 cm wide; bracts lanceolate to narrowly ovate, acute, truncate at the base, 2.5–3 cm long, 0.8–1 cm wide, longer than the capsules they subtend; leaves plane at the margins, remotely serrate, the teeth blunt or sharp. Inflorescence unbranched or branched. Floral tube 5–6 cm long. Buds narrowly oblong to lanceolate in outline, 0.8–1.1 cm long, 3.5–4 mm thick, often flushed with red, red striped at the junction of the sepals with the floral tube; apices of the sepals 2–3 mm long, erect or divergent. Petals very broadly obovate, exceeded in length by the stamens, 0.8–1.3 cm long. Anthers 6–7 mm long, ca. 1 mm broad. Filaments 7–10 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis; 5.5–7 cm long. Stigma lobes 4–5 mm long. Ovary 0.9–1.1 cm long. Capsule 1.5–2.5(–3) cm long, 3–4 cm thick. Seeds elliptic in outline, 1.5–1.8 mm long, 0.7–0.8 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: October–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Bolivia, Dept. Cochabamba, in fields and along the road from Cochabamba to Todos Santos, 26 km E of Cochabamba, 2,900 m, 3 Apr. 1968, *K. A. Santarius 1989* (MO-2155408, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 233): Known only from the vicinity of Cochabamba in Bolivia.

Specimens examined from cultivated plants:

BOLIVIA. COCHABAMBA: In fields and along the road from Cochabamba to Todos Santos, 26 km E of Cochabamba, 2,900 m, *Santarius 1975**, *1977**, *1980*, *1981*, *1984*, *1988**, *1989**, *1990*, *1991* (DUSS; *1989* also CTES, M; *1975*, *1977*, *1988*, *1989*, *1991* also MO).

Additional specimens examined:

BOLIVIA. COCHABAMBA: Cochabamba, 2,700 m, *Buchtien 2387* (US). Cercado near Cochabamba, 2,600 m, *Steinbach 8730* (BM, GH, K, LIL).

Oenothera pseudoelongata can be distinguished from *O. elongata* by its lower stature, smaller flowers, shorter floral tube, shorter capsules, and larger seeds. Usually it is also more densely pubescent. Its complexes are derived from *O. scabra* and *O. affinis*. As in *O. elongata*, there is evidence here of the exchange of genetic material between the two complexes since the *O. affinis*-like plants derived by crossing *O. affinis* with *O. pseudoelongata* have relatively short and thick capsules.

40. **Oenothera cordobensis** Dietrich, sp. nov.—FIGS. 94–95, 161, 206.

Herba annua, erecta, plerumque er rosulata, simplex vel e basi sursum ramosa, 4–10 dm alta. Plantae dense strigulosae denseque villosae, pilis erectis, praecipue circum inflorescentiam, alibi sparsiore. Folia caulina angustissime elliptica vel anguste elliptica, acuta, basi acuta vel truncata, sessilia, 5–10 cm longa, 1–2 cm lata; bractea lanceloata vel anguste ovata, acuta, basi truncata vel subcordata, sessilia, ad capsulas subtentas subaequalia, apicibus incurvatis, 2–3 cm longa, 0.8–1.5 cm lata; folia valde marginibus undulatis, irregulariter obtuseque

serrata. Inflorescentia simplex. Tubus floralis 1.5–2.5 cm longus. Gemmae ambito oblongae, virides, 0.8–1 cm longae, 3–4 mm crassae. Sepala saepe fusco-rubro punctata; apices sepalorum 2–3 mm longi, divergentes. Petala latissime obovata, 1.3–1.5 cm lata. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 0.8–1.2 cm longum. Capsula 1.8–2.5 cm longa, 3–4 mm crassa, extremi valvarum distincti, discreti, crenatique. Semina ambito late elliptica, 1–1.3 mm longa, 0.6–0.8 mm crassa, fusco-rubra punctata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, usually not forming a rosette, unbranched or branched from the base upward, 4–10 dm tall. Plant densely strigillose and densely villous with erect hairs, especially in the region of the inflorescence, and more sparsely so elsewhere. Cauline leaves very narrowly elliptic to narrowly elliptic, acute, acute to truncate at the base, sessile, 5–10 cm long, 1–2 cm wide; bracts lanceolate to narrowly ovate, acute, truncate to subcordate at the base, sessile, subequal in length to the capsules they subtend, the tips incurved, 2–3 cm long, 0.8–1.5 cm wide; leaves strongly undulate at the margins and irregularly serrate with blunt teeth. Inflorescence unbranched. Floral tube 1.5–2.5 cm long. Buds oblong in outline, green, 0.8–1 cm long, 3–4 mm thick. Sepals often flecked with dark reddish brown; apices of the sepals 2–3 mm long, divergent. Petals very broadly obovate, 1.3–1.5 cm long. Anthers 4–6 mm long. Filaments 7–9 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 2.5–4 cm long. Stigma lobes 4–5 mm long. Ovary 0.8–1.2 cm long. Capsule 1.8–2.5 cm long, 3–4 mm thick, with the ends of the valves free and crenate. Seeds broadly elliptic in outline, 1–1.3 mm long, 0.6–0.8 mm thick, flecked with dark red spots. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: December–April.

Type: Grown from seeds and cultivated in Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Argentina, Prov. Córdoba, Cuesta Blanca near Córdoba, Dec. 1961, *G. Göpel* (MO-2155198, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 227): Known only from a few localities west and south of Córdoba, Argentina.

Specimen examined from cultivated plants:
ARGENTINA. CÓRDOBA: Cuesta Blanca near Córdoba, *Göpel in 1961** (DUSS, M, MO).
Additional specimens examined:
ARGENTINA. CÓRDOBA: Alta Gracia, bank of Arroyo Alta Gracia, 600 m, *Hunziker 1209* (CORD, GH, LIL, RSA), *650* (CORD). Between La Carlota and Canals near San Severo, *Hunziker 11214* (CORD). Between Espinillo and Arroyo Messo near Río Cuarto, *Hunziker 11609* (CORD). Between Pan de Azúcar and Villa Allende near San Chico, *Hunziker 11932* (CORD). Sierra Chica, W slope of Cerro Uritorco, 1,600 m, *Hunziker 18037* (CORD). La Falda, *Hossens 172* pro parte (CORD). Dique, *Kuntze in 1891* (MO, NY).

Experimental hybrids to determine the parentage of *O. cordobensis* have not yet been carried out. Nevertheless, the red-flecked seeds and the absence of a rosette strongly suggest that the *Renneria*-complex might be attributed to *O. tafiensis*, which reaches the southeastern margin of its range in the Sierra de Córdoba. The red-flecked sepals and distinct, crenate valve ends of the capsule suggest *O. longiflora* and *O. ravenii*, the complexes of which are included in *O. parodiana*, frequent in the province of Córdoba.

41. **Oenothera siambonensis** Dietrich, sp. nov.—FIGS. 96–97, 162.

O. mollissima sensu Munz, Physis 11: 282. 1933, pro parte.
O. stricta sensu Munz, Physis 11: 285. 1933, pro parte.
O. parodiana "Siambon" Hecht, Indiana Univ. Publ. Sci. Ser. 16: 277. 1950; Cleland, Jap. J. Genet. 43: 332. 1968.

Herba annua, erecta, erosulata, e basi sursum ramosa, 6–12 dm alta. Plantae dense vel parce strigulosae, dense vel parce pilis longis brevibusque villosis praeditae, et circum inflorescentiam glanduloso-pubescentes. Folia caulina anguste oblonga vel angustissime elliptica ad elliptica, acuta, basi acuta vel rotundata, 4–15 cm longa, 1–3 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi truncata, sessilia, 2.5–3.5 cm longa, 0.5–1 cm lata; folia plana, irregulariter obtuseque serrata. Inflorescentia plerumque simplex. Tubus floralis 3–5.5 cm longus. Gemmae ambito lanceolatae, 1.5–2 cm longae, 3–4 mm crassae, saepe junctura sepalorum tubo florali rubro-fasciatae; apices sepalorum 1.5–3 mm longi, erecti. Petala latissime obovata, 2–2.5 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.2–1.5 cm longum. Capsula 2.5–3 cm longa, 3–4 mm crassa. Semina ambito late elliptica, plerumque fusco-rubro punctata, 1–1.2 mm longa, 0.5–0.6 mm crassa. Numerus gameticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, branched from the ground up, 6–12 dm tall. Plants densely to moderately strigillose, densely to moderately long- and short-villous, and with an admixture of glandular hairs in the region of the inflorescence. Cauline leaves narrowly oblong or very narrowly elliptic to elliptic, acute, acute to rounded at the base, 4–15 cm long, 1–3 cm wide; bracts narrowly lanceolate to lanceolate, acute, truncate at the base, sessile, 2.5–3.5 cm long, 0.5–1 cm wide; leaves plane at the margins, irregularly serrate with blunt teeth. Inflorescence usually unbranched. Floral tube 3–5.5 cm long. Buds lanceolate in outline, 1.5–2 cm long, 3–4 mm thick, often red striped at the junction of the sepals with the floral tube. Sepals yellowish green, sometimes flushed with red; apices of the sepals 1.5–3 mm long, erect. Petals very broadly obovate, 2–2.5 cm long. Anthers 7–8 mm long. Filaments 13–15 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 4–6.5 cm long. Stigma lobes 4–5 mm long. Ovary 1.2–1.5 cm long. Capsule 2.5–3 cm long, 3–4 mm thick. Seeds broadly elliptic in outline, usually flecked with dark reddish brown, 1–1.2 mm long, 0.5–0.6 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Argentina, Prov. Tucumán, edge of fields, Siambón above Tucumán, ca. 985 m, 11 Feb. 1939, *P. A. Munz 15472* (POM, holotype; GH, NY, isotypes).

Distribution (Fig. 240): Elevations of 500–2,000 m in the Argentine provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, and Córdoba.

Specimens examined from cultivated plants:

ARGENTINA. TUCUMÁN: Siambón near Tucumán, *Hecht 196-84** (CTES, DUSS, M, MO). Dry slope in Sierra de San Javier at "Ante Muerta" near Tucumán, *Göpel in 1961** (CTES, DUSS, M, MO). Between Villa Nouges and San Javier near Tucumán, *Göpel in 1961** (CTES, DUSS, M, MO).

Additional specimens examined:

ARGENTINA. JUJUY: Río Chico, *Holmberg in 1908* (SI). San Salvador de Jujuy, *Budín 93* (LIL). San Pablo, *Romero 17* (LIL). SALTA: Alemania near Guachipas, *Venturi 9847* (GH, K). TUCUMÁN: Tafí Viejo, 850 m, *Venturi 37* (LIL), *1325* (US). Above Tucumán, 915 m, *Munz 15465* (POM, US). Villa Nougés, *Munz 15464* (G); *Schreiter 706* (LIL). Siambón, *Lorentz & Hieronymus 753* (CORD, F, G, GOET, NY, POM); *Olea 308* (LIL); *Lillo*

FIGURE 243. Range of homozygous *Oenothera ravenii* subsp. *ravenii* (dots) and as a chromosomal complex in *O. hechtii*, *O. parodiana*, *O. pseudolongiflora*, *O. ravenii* subsp. *argentinae*, *O. ravenii* subsp. *chilensis*, *O. siambonensis*, *O. stricta*, and *O. villaricae* (hollow triangles).

1107 (LIL). Mountains above Siambón, 2,100 m, *Lillo 1772* (LIL). Trancas, 1,950 m, *N.N. 276* pro parte (LIL). Cerro de Campo near Burroyacú, 2,000 m, *Venturi 7748* (MO, POM, SI, US). Las Cuchillas near Burroyacú, 1,100 m, *Lillo 5309, 5310* (LIL). Escaba at Río Chico, 600 m, *Monetti 1665* (GH, LIL). La Cocha at Río Chaco near Cerro del Potrerillo, 700 m, *Bailetti 170* (LIL). CATAMARCA: Dep. Paclin, Balcosna Afuera, 35 km NW of La Merced, 1,300 m, *Hunziker & Di Fulvio 21164* (CORD). El Suncho, *Jörgensen 1440* (LIL, SI). LA RIOJA: Sierra Famatima, La Hoyada, 2,500 m, *Kurtz 15074* (CORD). Sierra Velazco, El Cantadero near La Mina, 2,300–2,400 m, *Hunziker 5219, 5244, 5285* (CORD). CÓRDOBA: La Esquina SE of Cerro Champaquí, *Hunziker 9662* (CORD). Sierra Grande, Copina, *Hunziker 11439* (CORD, RSA), *11437* (CORD). Pampa Achala, 900 m, *Hunziker 11912* (CORD). Sierra Achala, Casas Viejas, *Hieronymus 747* (CORD, F, GOET, US). Luyaba near San Javier, *Castellanos in 1927* (RSA).

The two chromosomal complexes in *O. siambonensis* are derived from *O. scabra* and *O. ravenii*. The latter has long since disappeared from the region where *O. siambonensis* occurs, which suggests that this species may be the oldest complex structural heterozygote resulting from the combination of *O. ravenii* with any other species. It is possible that the populations of *O. siambonensis* that occur in the province of Córdoba, like *O. tucumanensis*, have *O. tafiensis* subsp. *tafiensis* as their *Renneria* element. Since the characteristics of *O. scabra* versus *O. tafiensis* subsp. *tafiensis* are not sufficiently pronounced to make possible the separation of their respective hybrids with *O. ravenii*, however, the separation of *O. siambonensis* into two taxonomic species is a taxonomic impossibility, regardless of the derivation of the various populations grouped here.

42. **Oenothera brevipetala** Dietrich, sp. nov.—FIGS. 100–101, 163.

Herba annua, erecta, erosulata, e basi sursum ramosa, 10–15 dm alta. Plantae dense vel parce pilis brevibus longisque villosis denseque glandulosis praeditae. Folia caulina anguste elliptica, acuta, basi anguste cuneata vel acuta, breviter petiolata, 5–10 cm longa, 1–2 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi acuta vel rotundata, sessilia, 3–4 cm lata, 0.6–1 cm lata, quam capsula subtenta longiora; folia plana, remote obtuseque serrata. Inflorescentia simplex. Tubus floralis 4–4.5 cm longus. Gemmae ambito anguste lanceolatae, 0.8–1 cm longae, 2–3 mm crassae; apices sepalorum ca. 1.5 mm longi, erecti. Petala latissime obovata, 0.6–0.7 cm longa, quam anthera stylumque breviora. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 7–10 mm longum. Capsula 1.3–1.5 cm longa, 3–4 mm crassa. Semina ambito elliptica, 1.1–1.5 mm longa, 0.6–0.7 mm crassa, immaculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, branched from the ground up, 10–15 dm tall. Plants densely to moderately long- and short-villous and densely glandular-pubescent. Cauline leaves narrowly elliptic, acute, narrowly cuneate to acute at the base, short-petiolate, 5–10 cm long, 1–2 cm wide; bracts narrowly lanceolate to lanceolate, acute, acute to rounded at the base, sessile, 3–4 cm long, 0.6–1 cm wide, longer than the capsules they subtend; leaves plane at the margins, remotely serrate, the teeth blunt. Inflorescence unbranched. Floral tube 4–4.5 cm long. Buds narrowly lanceolate in outline, 0.8–1 cm long, 2–3 mm thick; apices of the sepals ca. 1.5 mm long, erect. Petals very broadly obovate, 0.6–0.7 cm long, exceeded in length by the anthers and the style. Anthers 6–8 mm long. Filaments 9–12 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 5–6 cm long. Stigma lobes 4–5 mm long. Ovary 7–10 mm long. Capsule 1.3–1.5 cm long, 3–4 mm thick. Seeds elliptic in outline, 1.1–1.5 mm long, 0.6–0.7 mm thick, not flecked with red. Self-

pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: November–April.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Bolivia, Dep. Cochabamba, edges of fields near Chacacolloa, ca. 7.5 km NE of Cochabamba, 2,550 m, 30 Mar. 1968, *K. A. Santarius 1972* (MO-2155223, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 234): Known only from the type locality.

Specimens examined from cultivated plants:
BOLIVIA. COCHABAMBA: Edges of fields near Chacacolloa, ca. 7.5 km NE of Cochabamba, 2,550 m, *Santarius 1972**, *1973* (DUSS; *1972* also M, MO).
Additional specimen examined:
BOLIVIA. COCHABAMBA: Liriuni, *Krapovickas 6994* (LIL).
Specimen from plants cultivated in garden:
Botanical Garden of Leningrad, from seeds of Bolivia sent by Cuming in 1847 (LE; as *O. brachypetala* F.M.).

The origin of the chromosomal complexes of *O. brevipetala* is not certain. The absence of strigillose pubescence in this species makes it highly probable that its *Renneria*-complex was derived from *O. scabra*, however, since that is the only species of the subsection in which plants that lack strigillose pubescence occur. *Oenothera indecora* may be the source of the other complex, judging from the small flowers and dense glandular pubescence. On the other hand, this complex might have been derived from *O. affinis* if one had assumed a strong evolutionary trend to small flower size in the complex heterozygote.

43. **Oenothera acuticarpa** Dietrich, sp. nov.—FIGS. 11, 92–93, 164, 207.

Herba annua, erecta, erosulata, e basi sursum ramosa, 7–10 dm alta. Plantae praecipue inferiore dense strigulosae, sparseque pilis longis brevibusque villosis ubique, etiam circum inflorescentiam glanduloso-pubescentibus praeditae. Folia caulina angustissime elliptica vel anguste, lanceolata, acuta, basi anguste cuneata vel acuta, sessilia, 6–15 cm longa, 0.8–2 cm lata; bractea anguste lanceolata vel lanceolata, acuta, basi acuta vel rotundata, sessilia, 4–5 cm longa, 0.8–1 cm lata; folia plana, irregulariter serrata. Inflorescentia simplex. Tubus floralis 4–6 cm longus. Gemmae ambito anguste oblongae vel lanceolatae, flavidae, junctura sepalorum tubo florali rubro-fasciatae, 1.5–2 cm longae, 4–5 mm crassae; apices sepalorum 1–2 mm longi, erecti. Petala latissime obovata, 1.8–2.5 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.5–1.8 cm longum. Capsula 2.5–3.5 cm longa, 3–4 mm crassa, in acuminem abrupte decrescens. Semina ambito elliptica, fusco-rubro punctata, 1–1.2 mm longa, 0.5–0.6 mm crassa. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, branched from the ground up, 7–10 dm tall. Plants densely strigillose, especially below, and sparsely long-villous and densely short-villous elsewhere, with a dense admixture of glandular pubescence in the inflorescence. Cauline leaves very narrowly elliptic to narrowly lanceolate, acute, narrowly cuneate to acute at the base, sessile, 6–15 cm long, 0.8–2 cm wide; bracts narrowly lanceolate to lanceolate, acute, acute to rounded at the base, sessile, 4–5 cm long, 0.8–1 cm wide; leaves plane at the margins, irregularly toothed. Inflorescence unbranched. Floral tube 4–6 cm long. Buds narrowly oblong to lanceolate in outline, yellowish, red striped at the junction of the sepals with the floral tube, 1.5–2 cm long, 4–5 mm thick; apices

of the sepals 1–2 mm long, erect. Petals very broadly obovate, 1.8–2.5 cm long. Anthers 9–11 mm long. Filaments 18–24 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 5.5–8 cm long. Stigma lobes 4–7 mm long. Ovary 1.5–1.9 cm long. Capsule 2.5–3.5 cm long, 3–4 mm thick, narrowed to an obvious point at the end (Fig. 11). Seeds elliptic in outline, flecked with dark reddish brown, 1–1.2 mm long, 0.5–0.6 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 10 and 2 bivalents* at meiotic metaphase I).

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Argentina, Prov. Tucumán, Villa Nougés near Tucumán, Dec. 1961, *G. Göpel* (MO-2155221, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 239): Known only from the type locality.

Specimen examined from cultivated plants:
ARGENTINA. TUCUMÁN: Villa Nougés near Tucumán, *Göpel in 1961** (DUSS, M, MO).
Additional specimen examined:
ARGENTINA. TUCUMÁN: Villa Nougés, *Pastore in 1916* (SI-4670).

The analysis of the chromosomal complexes of *O. acuticarpa* is simple. On self-pollination, homozygous individuals of *O. tafiensis* subsp. *parviflora* segregate in the progeny. The second complex is derived from *O. affinis* and F_1 hybrids between *O. affinis* and *O. acuticarpa* comprise two classes of plants, one identical to each of the parents. *Oenothera affinis* does not, however, appear in the selfed progeny of *O. acuticarpa*.

The strain of *O. acuticarpa* cultivated in Düsseldorf consistently forms a ring of 10 and 2 bivalents at meiotic metaphase I. Evidently the two free *Renneria* chromosomes are responsible for segregation of homozygous individuals and so for the failure of this species to become a complete complex heterozygote.

44. **Oenothera tucumanensis** Dietrich, sp. nov.—FIGS. 98–99, 165.

O. indecora sensu Munz, Physis 11: 281. 1933, pro parte; Amer. J. Bot. 22: 658. 1935, pro parte.

Herba annua, erecta, erosulata, simplex vel e basi sursum ramosa, 5–10(–13) dm alta. Plantae praecipue inferiore dense strigulosae, interdum sparse pilis longis praeditae, omnino pilis brevibus glandulosisque praeditae. Folia caulina angustissime elliptica vel elliptica, acuta, basi anguste cuneata vel acuta, plerumque breviter petiolata, 4–10 cm longa, 0.7–2 cm lata; bractea angustissime elliptica vel anguste lanceolata, acuta, basi acuta, plerumque sessilia, raro breviter petiolata, 3–5 cm longa, 0.5–1 cm lata, quam capsula subtenta longiora; folia plana vel marginibus manifeste undulatis, irregulariter obtuseque serrata. Inflorescentia plerumque ramosa. Tubus floralis 1.3–2.5 cm longus. Gemmae ambito oblongae vel lanceolatae, 0.6–0.9 cm longae, 2–3 mm crassae, flavo-virentes; apices sepalorum 1.5–2 mm longi, erecti vel divergentes. Petala latissime obovata, 0.5–1 cm longa. Stylus brevis, stigmate sub anthesi antheris circumdato. Ovarium 1.2–1.5 cm longum. Capsula 1.5–2.5 cm longa, 2–2.5 mm crassa. Semina ambito elliptica, 1–1.2 mm longa, 0.5–0.6 mm crassa, immaculata. Numerus gameticus chromosomaticus, $n = 7$; planta chromosomatice heterozygotica complexa.

Erect annual herb, not forming a rosette, simple or branched from the base upward, 5–10(–13) dm tall. Plants densely strigillose, especially below, sometimes sparsely long-villous, and short-villous and glandular-pubescent through-

FIGURE 244. Range of homozygous *Oenothera affinis* (filled triangles) and as a chromosomal complex in *O. acuticarpa*, *O. elongata*, *O. mollissima*, *O. montevidensis*, *O. parodiana* subsp. *brasiliensis*, *O. picensis*, *O. pseudoelongata*, and *O. pseudolongiflora* (circles).

out. Cauline leaves very narrowly elliptic to elliptic, acute, narrowly cuneate to acute at the base, usually short-petiolate, 4–10 cm long, 0.7–2 cm wide; bracts very narrowly elliptic to narrowly lanceolate, acute, acute at the base, usually sessile, rarely short-petiolate, 3–5 cm long, 0.5–1 cm wide, longer than the capsules they subtend; leaves plane or evidently undulate along the margins, irregularly bluntly toothed. Inflorescence usually branched. Floral tube 1.3–2.5 cm long. Buds oblong to lanceolate in outline, 0.6–0.9 cm long, 2–3 mm thick, yellowish green; apices of the sepals 1.5–2 mm long, erect or divergent. Petals very broadly obovate, 0.5–1 cm long. Anthers 3–5 mm long. Filaments 4–8 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 1.7–3.5 cm long. Stigma lobes 2–4 mm long. Ovary 1.2–1.5 cm long. Capsule 1.5–2.5 cm long, 2–2.5 mm thick. Seeds elliptic in outline, 1–1.2 mm long, 0.5–0.6 mm thick, not flecked with red. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: September–May.

Type: Grown from seeds and cultivated in the Botanical Garden of Düsseldorf, Germany, 4 Aug. 1972. Source: Argentina, Prov. Tucumán, in the rubble of the Río Salí near bridge on Ruta 9, E of Santa María de Tucumán, 420 m, 3 Mar. 1968, *K. A. Santarius 1657* (MO-2155219, holotype; CTES, DUSS, M, isotypes).

Distribution (Fig. 236): At elevations from 400 to 2,000 m in the Argentine provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja and Córdoba.

Specimens examined from cultivated plants:

ARGENTINA. TUCUMÁN: In the rubble of the Río Salí near bridge on Ruta 9, E of Tucumán, 420 m, *Santarius 1657*, 1664** (DUSS; *1657* also M, MO). Dry river bed between Villa Nougés and San Pablo near Tucumán, *Göpel in 1961** (DUSS).

Additional specimens examined:

ARGENTINA. JUJUY: Sierra de Calilegua, Ledesma, 700 m, *Venturi 5247* (LIL, SI, US). Three km S of San Salvador de Jujuy, 1,200 m, *Eyerdam et al. 22409* (GH, UC); *Arnow 3646* (MO). SALTA: Vicinity of Pampa Grande, *Nelson 12578* (CORD). TUCUMÁN: San Miguel de Tucumán, 450 m, *Lillo 8604* (F, LIL, MO, UC), *2066* (F, US), *474, 844, 912* (LIL); *Schreiter 1874, 2168, 3238* (LIL); *Meyer 12227* (RSA). Río Salí near Tucumán, 450 m, *898a* (BAA, US). Yerba Buena, *Wall in 1946* (S); *Sparre 480* (S); *Lillo 13248* (LIL); *Schreiter 1592* (LIL). Cruz Alta, 400 m, *Bailetti in 1917* (GH, LIL). Siambón, ca. 1,000 m, *Munz 15472* (NY). El Timbo near Burroyacú, 600 m, *Venturi 2231* (BM, LIL). Between Tafí Viejo and Muñecas, 600 m, *Schreiter 1879* (LIL). Monteros, León Rongues, *Herrera 578* (LIL). Sierra del Aconquija, *Humbert 10915* (P). CATAMARCA: Andalgala, *Jörgensen 1054* pro parte (GH, LIL, MO, SI, US); *Schickendantz 128* (B, destroyed, F photograph, POM, SI). City of Catamarca, *Picinnini 68205* (BAB); *Castillon in 1910* (SI-26724). Yacutula near Belén, *Schickendantz in 1887, 1879* (CORD); *White 18* (BM). Dep. El Alto, at Ruta 64 near El Portezuelo, *Sublis & Artico 53* (CORD). Dep. Ambato, El Rodeo, 1,800 m, *N.N. in 1949* (LIL-315929, LIL-318578). Belén, between Quebrada de los Potrerillos and El Rodeo, 2,700 m, *Sleumer & Vervoorst 2472* (LIL). Dep. Santa María, between the rivers, 2,000 m, *Peirano in 1933* (GH, LIL). LA RIOJA: Sierra Velasco, Yacuchi, *Kurtz 15415* (CORD). CÓRDOBA: Dep. Punilla, La Falda, *Kurtz 10167* (CORD).

Judging from the fact that *O. peduncultifolia* × *O. indecora* subsp. *bonariensis* produces plants that are phenotypically very similar to *O. tucumanensis*, these are its parents. This species therefore provides an example of a complex heterozygote that arose in the presence of its two parents, and still grows together with them. The plants from Córdoba might have originated following hybrid-

ization between *O. tafiensis* subsp. *tafiensis*, which occurs in the mountains of Córdoba, and the widespread *O. indecora*. Notwithstanding this possibility, they are indistinguishable from the type and it is therefore not possible to regard them as a distinct species taxonomically.

45. **Oenothera punae** Kuntze, Rev. Gen. Pl. 3(2): 99. 1893.—Figs. 84–85, 166, 184, 208.

Onothera kuntziana H. Lév., Monogr. Onoth. 359. 1909; Bull. Acad. Int. Géogr. Bot. 19: 319. 1909, illeg. subst. for *O. punae* Kuntze.
Raimannia punae (Kuntze) Sprague & Riley, Bull. Misc. Inform. 1921: 201. 1921.
Oenothera nana sensu Munz, Physis 11: 280. 1933, pro parte; Amer. J. Bot. 22: 650. 1935, pro parte.
O. nana sensu Macbride, Field Mus. Nat. Hist., Bot. Ser. 13(4): 539. 1941, pro parte.

Annual to perennial herb, forming a rosette, with a prostrate main stem and prostrate branches arising from the rosette, the main stem rarely obliquely arising from the ground, the branches 5–25 cm long. Plants exclusively densely strigillose. Rosette leaves linear to very narrowly elliptic, acute, narrowly cuneate at the base, short-petiolate, 2–5 cm long, 1–3(–5) cm wide; cauline leaves linear to very narrowly elliptic, acute, narrowly cuneate at the base, sessile, 1.5–4 cm long, 1–3(–5) cm wide; bracts linear to very narrowly elliptic, acute, narrowly cuneate to acute at the base, sessile, 1.5–3(–4) cm long, 1–3(–5) cm wide; leaves plane or evidently undulate at the margins, irregularly bluntly toothed. Inflorescence unbranched. Floral tube 5–10(–15) mm long; buds oblong to broadly elliptic in outline, green or yellowish green, often red striped at the junction of the sepals with the floral tube, 3–4 mm long, 2–3 mm thick. Sepals often flecked with dark red; apices of the sepals 0.5–1 mm long, mostly erect. Petals very broadly obovate, often flushed with red, 0.4–1 cm long. Anthers 2.5–4 mm long. Filaments 2.5–6 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 0.8–1.5(–2) cm long. Stigma lobes 1.5–2 mm long. Ovary 5–10 mm long. Capsule 1.2–1.7 cm long, 2.5–3.5 mm thick, cylindrical or slightly enlarged towards the base. Seeds broadly elliptic to rotund in outline, 0.8–1.2 mm long, 0.7–0.9 mm thick. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14* at meiotic metaphase I). Flowering time: Northern area, October–March; southern area, November–April.

Type: Bolivia, Dep. Oruro, at the Challapata railroad station on high plateau of Puno, 11 Mar. 1892, *O. Kuntze* (not located).

Distribution (Fig. 238): At elevations from 2,000 to 4,700 m in the Andes; in the southern departments of Peru, including Cuzco, Arequipa, and Puno; in the departments of La Paz, Cochabamba, Oruro, Potosí, and Tarija in Bolivia, but not yet seen from Chuquisaca; and in the provinces of Jujuy, Salta, Tucumán, Catamarca, and La Rioja in Argentina.

Specimens examined from cultivated plants:

Peru. puno: Waste places ca. 2 km SE of Zepita, sandy soil, 3,820 m, *Santarius 2034** (DUSS, M, MO). Dry grasslands, ca. 6 km NNW of Puno, below road to Juliaca, 3,850 m, *Santarius 2041**, *2042** (DUSS; *2041* also MO). Sandy slopes above Chimu, ca. 8 km SE of

Puno at the road to Chucuito, 3,900 m, *Santarius 2044** (DUSS, M, MO); 4,000–4,100 m, *Santarius 2046, 2047, 2048, 2055* (DUSS; *2046* also M; *2046, 2048* also MO).

BOLIVIA. LA PAZ: La Paz, dry slopes of the Cerro Calvario ca. 100 m N of the chapel, 3,800 m, *Santarius 2008–2012, 2013*, 2014*, 2015** (DUSS; *2008* also CTES, M; *2008, 2010, 2012–2015* also MO). COCHABAMBA: Ca. 35 km E of Cochabamba on the road to Todos Santos, dry grasslands, 3,000 m, *Santarius 1997*, 2000, 2001*, 2002** (DUSS; *2001, 2002* also MO).

ARGENTINA. JUJUY: Steppe ca. 1 km S of Abra Pampa, ca. 100–150 m W and NW of the cemetery, 3,485 m, *Santarius 1886* (DUSS, MO). On sandy rubble in the steppe along road from La Quiaca to Yaví, ca. 3 km E of La Quiaca, 3,550 m, *Santarius 1888, 1898* (DUSS). TUCUMÁN: Rubble in bed of Río Angostura ca. 5 km N of Tafí del Valle, 2,000–2,550 m, *Santarius 1742*, 1743* (DUSS, MO; *1742* also CTES, M).

Representative specimens examined:

PERU. AREQUIPA: Prov. Condesuyos, Chuquibamba, 3,800 m, *Stafford 1178* (BM). CUZCO: Prov. Anta, El Chaccan near Cillapuyu, 3,605 m, *Brunel 240* (MO). PUNO: Puno, 4,000 m, *Soukup 105* (F). Arapa near Azángaro, 3,900 m, *Aguilar 222, 225* (USM). Conima near Huancané, 3,900 m, *Aguilar 224* (USM). Moho near Huancané, *Aguilar 226* (USM). Amantani near Lake Titicaca, 3,900 m, *Aguilar 229, 233* (USM). Juliaca, 4,250 m, *Stafford 271* (K). Macusani near Carabaya, 4,360 m, *Vargas 7126* (MO, RSA). Lake Titicaca, 3,820 m, *Vargas 1275* (F). Cayachita, 4,450 m, *Sharpe 14* (K). Huascapata, 3,900 m, *Aguilar 223* (USM).

BOLIVIA. LA PAZ: Mountain slopes near La Paz, 3,800 m, *Buchtien 644a* (GH, NY, US). La Paz, *Wolsterholme 9* (K). Cerro Calvario near La Paz, 3,800 m, *Parodi 10107* (BAA, POM), *10120* (MO). Prov. Larecaja, road to Coroico, 4,000 m, *Mandon 631* (G, K, NY, P, S, W). Prov. Ingari, Hacienda San José on peninsula Taraco, *Hammarlund 164* (S). Laja, *Hill 158* (K). Above Guaqui, *Hill 159* (K). Hills near Huatajata at Lake Titicaca, 4,000 m, *Heine in 1954* (M). Calachaca W of Pucarani, 3,900 m, *Herzog 2474a* (L). Upper Araca valley near Viloco, 3,800 m, *Herzog 2334b* (L). Pacajes: Corocoro, 4,000 m, *Asplund 2420* (UPS). ORURO: Cona Cona station on the line from Oruro to Cochabamba, 4,250 m, *Brooke 5214* (BM). 141 mi from La Paz, 3,950 m, *Brooke 5254* (BM). Challapata, 3,900 m, *Asplund 5972* (US). Prov. Cercado, Hacienda Huancaroma near Eucaliptus, 3,800 m, *Hammarlund 119, 120* (S). Viloco, 100 mi from Oruro, road to Eucaliptus and Cascata near Araca, *Brooke 5329A* (BM). POTOSÍ: 4,000 m, *Cardena 125* (GH). Uyuni, 4,000 m, *N.N.* (S). TARIJA: Escayache near Tarija, *Fiebrig 3030* (BM, F, GH, K, LD, LE, LIL, NY, S, SI, US). Department unknown: Between Quebrada Honda and Salitre, 4,000 m, *Fries 1028* (S).

ARGENTINA. JUJUY: Cerro Negro near Yaví, 4,000 m, *Meyer 33730* (LIL). San Gregorio near Tilcara, 3,400 m, *Sleumer 3133* (LIL). Laguna Tres Cruces near Cochinoca, 3,700 m, *Claren in 1901* (CORD, S). La Rinconada, 3,800 m, *Claren in 1901* (CORD, S). Cajas, 35 km E of La Quiaca, 3,900 m, *Hjerting et al. 123* (C). Mina Águilar, 4,700 m, *Schwabe 558* (BAA), 4,300 m, *452, 471* (BAB); *Petersen & Hjerting 116* (C, LIL); *Cabrera & Frangi 20713* (LP); *Cabrera 9223* (LP). Quebrada de Cajos near Yaví, 4,000 m, *Cabrera 7845* (LP). SALTA: Lizoite near Sta. Victoria, 3,340 m, *Meyer & Bianchi 33738, 33739* (LIL). Top of Obispo near Cachi, 3,720 m, *Rosmero in 1947* (LIL). Between Trancas and Cafayate, *Haumann 31-1521* (BA). Banks of Río Colorado near Cafayate, *Krapovickas & Cristóbal 20686* (CTES). TUCUMÁN: Tafí, 2,200 m, *Lillo 4315, 7779* (LIL), *7500* (GH, LIL, UC); *Rodriguez 302* (GH, LIL, SI). Lara at Cerro Calchaquies, *Baer 10* (LIL, POM). La Ciénaga, 2,500 m, *Lillo 4034, 4072, 1212* (LIL); *Lorentz & Hieronymus* (CORD, GOET). Río Blanco near Cerro Muñoz, 2,500 m, *Lillo 3034, 8867* (LIL). Mesopotamia, *Castillon 182, 2262* (LIL). La Puerta, 4,000 m, *Parodi 10812* (POM). Cuesta de los Cordones, 3,800 m, *Schreiter 7059* (LIL, MO); *Burkart 5337* (POM, SI). Tafí del Valle, 2,000 m, *Sparre 5648* (LIL); *Araque & Barkley 19AR162* (F, LIL); *Wall in 1946* (S); *Dinelli 21518* (BAB); *Sleumer 146* (B, LIL). Río Churqui, 2,000 m, *Lillo 7655* (LIL). Infiernillo, 3,500 m, *Sparre 6032* (LIL); *Hjerting et al. 9284* (C); *Sparre 1094* (S); *Burkart 22081* (SI); *Cristóbal 523* (LIL, UC); *Krapovickas & Cristóbal 20506* (CTES); *Krapovickas et al. 21851* (CTES, MO). Chorro near Trancas, 4,000 m, *Schreiter 663* (LIL). CATAMARCA: Portezuelo de Yutiyaco, Cerro del Campo Grande, *Schickendantz 315* (CORD, GOET). Capillitas, *Schickendantz* (CORD). Sierra de Ambato, El Rodeo to Casa de Cubas at Cerro Manchado, 3,300–3,400 m, *Hunziker & Di Fulvio 19803, 19918* (CORD). Dep. Sta. María, Sierra de Aconquija, 3,100 m, *Peirano in 1933* (LIL-80204). LA RIOJA: Sierra de Famatima, Vallecito, *Hieronymus & Niederlein 713* (CORD). La Encrucijada, *Hieronymus & Niederlein 481* (CORD). Portezuelo del Caño

de Tocino, 3,350 m, *Krapovickas & Hunziker 5303* (BAB, CORD). Puerto Sta. Rosa, 3,100 m, *Hunziker 1885* (CORD, POM). Mesada de Casablanca, *Krapovickas & Hunziker 5262* (BAB, CORD). Top of Espíritu Santo, *Jiménez 15243* (CORD). Mina San Juan, 3,050–3,200 m, *Kurtz 13590* (CORD). El Volcán, *Kurtz 14653* (CORD, MO). La Batea, 2,900 m, *Hunziker 1861* (CORD).

Oenothera punae provides a classical example of our often fragmentary knowledge of plant distributions in the high Andes. It is collected time and time again along the Andean highways, but very seldom in the vast tracts of land that lie between. It is, for example, inconceivable that the species should be absent in the department of Chuquisaca, Bolivia. Also, the very few collections available from southern Bolivia (*Fiebrig 3030*) clearly do not provide an accurate indication of the true situation. Perhaps the scanty representation of *O. punae* in herbaria is also related to the small flowers and generally inconspicuous nature of this species.

As in the other highly condensed Andean species of the subsection, *O. nana*, *O. punae* has complexes from at least three species of series *Renneria*: *O. peruana*, *O. versicolor*, and *O. lasiocarpa*. These are in *O. punae* combined with a genome derived from *O. indecora* subsp. *boliviensis* of series *Allochroa*. One striking fact is that the glandular pubescence of *O. indecora* is completely absent in *O. punae*.

In populations of *Oenothera nana* and *O. punae* it is possible to catch a glimpse of the very active and rapidly evolving relationship between these two taxa. They frequently grow together, and progenies from seeds taken from a single plant in the wild often consist of two or even three distinct and sharply delimited sorts of plants. Either of the *Renneria* complexes found in *O. nana* may be present interchangeably in *O. punae*. If one designates the *nana*-complexes respectively *Ra* and *Rb*, and the *indecora*-complex of *O. punae C*, the following genetic constitutions were recognized among the collections made by Professor Santarius:

Santarius 1886—	Ra–Rb	+ Ra–C	+ Rb–C
Santarius 1888—	Ra–Rb		+ Rb–C
Santarius 1997—		Ra–C	+ Rb–C
Santarius 2001—	Ra–Rb	+ Ra–C	+ Rb–C
Santarius 2008—		Ra–C	+ Rb–C
Santarius 2010—		Ra–C	+ Rb–C
Santarius 2012—		Ra–C	+ Rb–C
Santarius 2013—		Ra–C	+ Rb–C
Santarius 2014—		Ra–C	+ Rb–C
Santarius 2055—	Ra–Rb		+ Rb–C

Voucher specimens documenting these results are deposited in the Herbarium of the Botanisches Institut at the University of Düsseldorf (DUSS). Among the herbarium material I have examined from other institutions, the following combinations are also represented:

Fiebrig 3030 (US)— Ra–Rb + Rb–C
Fries 1028 (S)— Ra–Rb + Ra–C
Hammarlund 119 (S)—Ra–Rb + Rb–C

The two different sorts of *O. punae* can be distinguished by the shape of their mature capsules. In the first, the capsules are cylindrical, whereas in the second, they are somewhat broadened at the base and usually also somewhat shorter. It is however not desirable to separate them taxonomically as independent species owing to their great similarity and close genetic relationships as well as to the presence of intermediate plants.

These facts can only be interpreted to indicate a tendency for the exchange of genomes between species growing together, as has already been noted from *O. sandiana* and *O. parodiana*. Evidently the system is balanced so that all combinations give a ring of 14 chromosomes at meiotic metaphase I, since no plants with smaller rings have been detected among the progenies that have been cultivated so far.

In such a system, crossing over can lead to the exchange of genes between more than two distinct genomes, a system of high evolutionary potential in enhancing the variability of the overall population and hence its capacity to produce new recombinants in response to the selective pressures of the extreme environments where these plants grow.

B. Subsection RAIMANNIA

Oenothera sect. **Oenothera** subsect. **Raimannia** (Rose) Dietrich, stat. nov. Based on *Raimannia* Rose, Contr. U.S. Natl. Herb. 8: 330. 1905. TYPE: *Oenothera laciniata* Hill.

Oenothera subgen. *Raimannia* (Rose) Munz, Amer. J. Bot. 22: 645. 1935; N. Amer. Fl., ser. 2, 5: 104. 1965, pro parte.

This is a primarily North American group of approximately eight species. Only one species, *Oenothera laciniata*, reaches South America. The description and full synonymy for this subsection will be given in connection with a forthcoming revision of the group as a whole.

46. **Oenothera laciniata** Hill, Hort. Kew. 172/4, *tab. 6.* 1768.

A complete description of this species is not given here, pending the completion of current investigations of the species of subsect. *Raimannia.*

Type: From the Carolinas, cultivated at the Royal Botanic Gardens, Kew (BM? Not seen).

KEY TO THE SUBSPECIES

1. Sepal tips 0.1–1 mm long, erect .... 46a. subsp. *pubescens*
1'. Sepal tips 1–2 mm long, more or less spreading .... 46b. subsp. *laciniata*

46a. **Oenothera laciniata** subsp. **pubescens** (Willd. ex Spreng.) Munz, North Amer. Fl., ser. 2, 5: 109. 1965; Opera Bot., Ser. B, 3: 40. 1974.—FIGS. 167, 191–192.

O. pubescens Willd. ex Spreng., Syst. Veg. 2: 229. 1825.
O. stuebelii Hieron., Bot. Jahrb. Syst. 21: 327. 1895. TYPE: Ecuador, Prov. Imbabura, Loma and vicinity of La Canaballa, 2,000–2,300 m, 1 July 1871, *A. Stübel 161 b* (B, destroyed, F-14013 photograph).
O. laciniata sensu Munz, Contr. Gray Herb. 75: 20. 1925.
O. laciniata var. *nocturna* (Jacq.) Munz, Amer. J. Bot. 22: 656. 1935, pro parte.
O. laciniata var. *pubescens* (Willd.) Munz, Amer. J. Bot. 22: 656. 1935.
O. verrucosa Munz, Amer. J. Bot. 22: 657. 1935, pro parte.
O. pennellii Munz, Leafl. West. Bot. 2: 156. 1939. TYPE: Mexico, Nuevo León, Sierra Madre Oriental, from grassy slope, Mt. "El Infiernillo," Pablillo, southeast of Galeana, 29 June 1934, *F. W. Pennell 17139* (US-1640419).

Plants annual to perhaps perennial, erect, forming a rosette, unbranched or few to many branched from the base, 0.5–5 dm tall; side branches from the rosette prostrate to arcuate-ascending. Plants densely to very sparsely strigillose and densely to sparsely villous, very sparsely to sparsely glandular-pubescent only on the sepals and floral tube. Rosette leaves narrowly oblanceolate, acute, gradually narrowed to the petiole, 5–10 cm long, 0.5–1 cm wide; cauline leaves very narrowly elliptic to lanceolate or narrowly oblanceolate, acute, the base truncate to subcordate, sessile or short-petiolate, 3–8 cm long, 0.5–1.5(–2.5) cm wide; bracts narrowly lanceolate to lanceolate, acute, attenuate to truncate at the base, sessile or short-petiolate, 2.5–6 cm long, 0.5–1.5(–2) cm wide; all leaves deeply sinuate-toothed to subentire, plane to prominently undulate at the margins. Inflorescence simple or branched; flowers erect, the mature buds nodding, the younger ones erect. Floral tube 2–3.3 cm long. Buds narrowly oblong to oblong in outline, yellowish green, red striped at the zone of attachment of the sepals, often generally flushed with red and flecked with reddish brown, 5–15 mm long, 3–5 mm wide; sepal tips 0.1–1 mm long, erect. Petals broadly obovate to very broadly obovate, yellow, 5–15 mm long. Anthers 3–9 mm long. Filaments 6–12 mm long. Style 2.8–4 cm long, the lobes of the stigma 2.5–5 mm long; style surrounded by the anthers at anthesis, these shedding pollen directly on it. Ovary 1–2 cm long. Capsule (2–)3–4 cm long, 2.5–4 mm thick, arising from the stem at an acute angle, straight or curved; valves of the capsule curved outward following dehiscence. Seeds broadly elliptic to rotund in outline, 0.9–1.3 mm long, 0.6–1 mm thick, brown. Gametic chromosome number, $n = 7$ (ring of 14* or ring of 12 and 1 bivalent** at meiotic metaphase I). Flowering time: throughout the year. (The description is based exclusively on South American plants.)

Type: Ecuador, *A. von Humboldt*, Herb. Willdenow 7177 (B, holotype, F-14008 photograph).

Distribution (Fig. 238): Andes of Colombia, Ecuador and Peru south to the province of Junín, elevation 2,000–3,900 m; in North America from Western Texas to Arizona south to Guatemala.

Specimens examined from cultivated plants:

PERU. JUNÍN: Valley of Río Mantaro, stony places between the river and the railway ca. 1 km S of the station of Pachacayo, ca. 45 km S of La Oroya, ca. 3,650 m, *Santarius 2190**, *2191**, *2192**, *2195**, *2196**, *2197**, *2198**, *2200**, *2202** (DUSS; *2190, 2198* also MO; *2190* also CTES). AYACUCHO: Waste places and slopes W of Ayacucho, ca. 2,900 m, *Santarius 2235**, *2236**, *2237**, *2238*** (DUSS; *2235* also MO). LIMA: Rimac valley, between Matu-

cana and Surco, on road and dry slopes between km 74.9 and 76.1, ca. 2,200 m, *Santarius 2326** (DUSS).

Additional South American specimens examined:

COLOMBIA. CUNDINAMARCA: Facacativá, 2,650 m, *Schneider 1007* (S). Usaquén, 2,650 m, *Schneider 340* (S). VALLE: Río Bugalagrande, from La Parilla to La Machuca, Loma of Barragán, 2,660–2,750 m, *Cuatrecasas 20704* (F). NARIÑO: "La Chorrera," 2,600 m, *Fernández & Mora 1217* (NY). Pasto, Botanical Garden of the University, 2,900 m, *Porter 1042* (GH). Without exact locality: Nova Grenada, *Triana in 1851–1857* (US).

ECUADOR. CARCHI: Tulcán, 2,700 m, *Harling 4028* (S, UPS). IMBABURA: Lake Cuicocha, *Summers 821* (F, GH); *Prescott 218* (NY). Hacienda "Rosa Pamba" near Otavalo, 2,850–3,000 m, *Solís 8028* (F). PICHINCHA: Guápulo near Quito, 2,650 m, *Asplund 6284* (G, K, LD, NY, P, R, UPS, US). Vicinity of Quito, 2,800 m, *Solís 1529* (M), *10039* (F); *Hall 1* (K); *Benoist 2107, 4303* (P); *Couthouy in 1855* (GH, NY); *Karsten* (LE). Lake Magdalena near Quito, *Hartweg 982* (BREM, G, K, LD, NY, P). Nayón, *Benoist 2616* (P). Puéllaro, 2,100 m, *Solís 16492* (F). Valley of Tumbamba, Quebrada del Machángara, 2,800 m, *Firmín 67* (F, US). W of Nono, 2,700 m, *Harling et al. 10248* (RSA). El Llalo, ca. 3,650 m, *Balls 5841* (K). NAPO: Paluquillo near Papallacta, Cerro Antisana, *Grubb et al. 190* (NY). COTOPAXI: Plateau of Latacunga and vicinity of Volcán Cotopaxi, ca. 2,250 m, *N.N. in 1858* (M). Volcán Cotopaxi, 2,800–3,500 m, *N.N. in 1858* (M). TUNGURAHUA: 10 km S of Mocha, 3,300 m, *Harling et al. 6892* (RSA). Between Leito and La Cima, 2,700–3,000 m, *Solís 9020* (F). Between Casingana and Chilcaloma, 2,900–3,300 m, *Solís 9104* (F). BOLÍVAR: Between Guaranda and Vinchoa, 2,800 m, *Solís 5959* (F). CHIMBORAZO: Sandy plains near Riobamba, 2,900 m, *Rimbach 420* (F, NY, S, UC); *Spruce 5039* (C, LE, G, GH, K, LD, P); *Rivet 142, 149* (P). Valley of Puaranda, S of Chimborazo, 2,500–2,900 m, *Wagner 3* (M). El Carmén near Sibambe, 2,450 m, *Solís 5551* (F). Javiñac, ca. 15 km from Penipe, 2,800 m, *Lugo 555* (RSA). Slopes of Cerro Chiguazo, 2,900 m, *Lugo 509* (RSA). El Retén, 20 km S of Cebades, 3,200 m, *Harling et al. 6618* (RSA). CAÑAR: Tambillo, 2,785 m, *Solís 1531* (M). Guamate near Tambo, 3,020 m, *Solís 1532* (M). AZUAY: Vicinity of Cuenca, near union of the rivers Tarqui and Yanuncay, 2,700–2,900 m, *Camp 2637* (NY, RSA, US). PROVINCE UNKNOWN OR WITHOUT EXACT LOCALITY: Liusa, *Rose & Rose 23907* (US). Near Catocollas, *Mille 398* (US). Ecuador, *Weydahl in 1957* (S); *Bonpland 2011* (P); *Fraser in 1860* (G).

PERU. AMAZONAS: Chacapoyas, *Matthews* (NY). ANCASH: Baños de Chancos near Huaráz, ca. 2,950 m, *Sandeman 4617* (K). HUÁNUCO: Mito, 2,950 m, *Macbride & Featherstone 1528* (F, G, GH, S, US). LA LIBERTAD: Between Pampa and Yamobamba, ca. 70 km E of Trujillo, 3,050 m, *Conrad 2712* (MO). LIMA: Rimac, *Saratier 1397* (K). Lima, *Castelnau in 1847* (P); *Cuming 1079* (K). JUNÍN: El Mantaro near Jauja, *Ochoa 1000* (GH). Between Palca and Codapata near Tarma, 2,600–2,800 m, *Velarde 654* (RSA). WITHOUT EXACT LOCALITY: *Matthews in 1862* (NY); *Schweinitz* (K).

Oenothera laciniata can be distinguished from all other South American species of the genus by its nodding buds and also by the pitting of its seed coat (Fig. 191), characteristics that suggest a relationship with the North American *O. grandis* (Rose) Smyth (Fig. 194). If *O. laciniata* subsp. *pubescens* has indeed contributed a genome to both *O. nocturna* and *O. arequipensis*, one would think that there would be no barrier to hybridization between this entity and *O. featherstonei* and *O. verrucosa*, respectively. When *O. nocturna* was used as the female parent in crosses with *O. laciniata* subsp. *pubescens*, however, the F_1 hybrids were semiviable albinos that died after the production of only a few leaves. The reciprocal cross produced only empty seeds (Stubbe, pers. comm.), and the matter clearly needs further investigation.

46b. **Oenothera laciniata** subsp. **laciniata** Munz, N. Amer. Fl., ser. 2, 5: 109. 1965. [Synonymy not given.]

Plants with much less anthocyanin than in subsp. *pubescens*. Sepal tips 1–2 mm long, perhaps longer in North American specimens, erect to divergent. Se-

pals not flecked with red spots. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I).

Distribution: North American. Naturalized at one locality each in Paraguay, where it was collected once in cultivated ground in 1958, and in Brazil, where it was collected once in 1898.

Specimens examined:
BRAZIL. RIO GRANDE DO SUL: Pôrto Alegre, *Reineck in 1898* (LD).
PARAGUAY. SAN PEDRO: Alto Paraguay, primavera, cultivated, 1958, *Woolston 1024* (NY, S, SP, UC).

47. **Oenothera drummondii** Hooker, Bot. Mag. 61: *tab. 3361.* 1834; Munz, N. Amer. Fl., ser. 2, 5: 107. 1965. [Synonymy not given.]

Perennial herb, erect or ascending, forming a rosette, with a branched main stem and prostrate to arcuate-ascending side branches from the rosette, 2–6 dm tall. Plants densely gray-strigillose and very sparsely appressed to erect long-villous, also glandular-pubescent only on the sepals and floral tube. Rosette leaves narrowly oblanceolate, acute, gradually narrowed to the petiole, distantly sinuate-toothed, 6–18 cm long, 1–1.5 cm wide; cauline leaves narrowly elliptic to oblanceolate, acute, narrowly cuneate at the base, sessile or short-petiolate, remotely toothed, the teeth obtuse, to entire, rarely with large curved teeth near the base, 1.5–8 cm long, 0.5–2 cm wide; bracts narrowly elliptic, acute, narrowly cuneate at the base, sessile, remotely toothed, the teeth obtuse, to entire. Inflorescence branched. Flowers erect; young buds with a straight floral tube, the older ones with the floral tube curved upward. Floral tube 3–5 cm long. Buds lanceolate in outline, light green, 1.5–3 cm long, 0.5–1 cm thick; sepal tips 1–2 mm long, erect. Petals very broadly obovate, 2.5–5 cm long, yellow. Anthers 7–10 mm long. Filaments 12–21 mm long. Style 5–8 cm long. Stigma elevated above the anthers at anthesis; stigma lobes 4–8 mm long. Ovary 1–2.5 cm long. Capsule cylindrical, 3–5 cm long, 2–2.5 mm thick, arising from the stem at an angle. Seeds elliptic in outline, 1–1.5 mm long, 0.5–0.8 mm thick. Gametic chromosome number, $n = 7$ (7 bivalents or small rings at meiotic metaphase I).

Type: United States, Texas, Rio Brazos, *Thomas Drummond 26* (K, holotype; G, isotype).

Distribution: Texas to Veracruz, along the shores of the Gulf of Mexico; widely naturalized elsewhere, as near Supe in the vicinity of Lima, Peru, the only station known in South America.

Specimens examined:
PERU. LIMA: Prov. Chancay near Supe, in a wash near the beach at sea level, 1938, *Eyerdam 9067* (G, GH, K, MO, UC). Just N of Supe, in field near highway, sandy soil, not too dry, 1939, *Goodspeed 17362* (F, G, GH, K, MO, S, UC).

C. Subsect. EUOENOTHERA

Oenothera sect. **Oenothera** subsect. **Euoenothera** (Torr. & A. Gray) Dietrich, stat. nov. Based on *Oenothera* subg. *Euoenothera* Torr. & A. Gray, Fl. N.

Amer. 1: 492. LECTOTYPE: *Oenothera biennis* L.; Munz, N. Amer. Fl., ser. 2, 5: 120. 1965.

The description and full synonymy of this subsection will be given subsequently. It is entirely North American but widely naturalized throughout the temperate regions of the world.

48. **Oenothera erythrosepala** Borbás, Magyar Bot. Lapok 2: 245. 1903; Munz, N. Amer. Fl., ser. 2, 5: 130. 1965.

O. glazioviana Micheli in Martius, Fl. Bras. 13(2): 178. 1882. TYPE: Brasil, Rio de Janeiro, Tijuca, 7 Feb. 1868, *A. Glaziou 2568* (P, holotype, F-38382 photograph; BR, G, isotypes).
O. fusiformis Munz & Johnston, Contr. Gray Herb. 75: 21. 1925. TYPE: Ecuador, Prov. Loja, between El Tambo and La Toma, 1,000–2,200 m, 3 Sep. 1923, *A. S. Hitchcock 21350* (US-1196309, holotype; GH, NY, isotypes).
O. lamarckiana auct. mult., non Séringe in DC., Prodr. 3: 47. 1828.
O. grandiflora sensu Munz, Opera Bot., Ser. B, 3: 40. 1974, non L'Hér. ex Aiton, Hort. Kew. 2: 2. 1789.

Plants usually biennial, forming a rosette, erect, with simple or much-branched main stem and arcuate-ascending side branches from the rosette, 1–12 dm tall. Plants strigillose and coarsely erect-villous, some to many of the hairs with a red pustule at their base, the inflorescence mixed villous and glandular-pubescent. Rosette leaves narrowly lanceolate to oblanceolate, acute to subobtuse, gradually narrowed to the petiole, 13–30 cm long, 3–5 cm wide; cauline leaves narrowly elliptic to lanceolate, acute to almost obtuse, rather abruptly narrowed to the petiole, the uppermost sessile, 5–12 cm long, 2.5–4 cm wide; bracts lanceolate to narrowly ovate, acute, narrowly cuneate at the base, 1–3 (–5) cm long, 0.7–3.2 cm wide; all leaves undulate at the margins and sinuate-toothed to serrulate, sometimes reddish along the midrib. Inflorescence simple or branched. Floral tube 3.5–5 cm long. Buds lanceolate in outline, 3–4 cm long, 0.7–0.9 cm thick, often flushed with red. Sepals 2.8–4.2 cm long, 0.4–0.8 mm wide, red striped along the midrib; sepal tips 5–8 mm long, spreading. Petals very broadly obovate, retuse, 3.5–5 cm long. Anthers 10–12 mm long. Filaments 1.7–2.5 cm long. Style 5–8 cm long, the stigma held above the anthers at anthesis, its lobes 5–7 mm long. Ovary 0.7–1.2 cm long. Capsule narrowly lanceolate in outline, 2–3 cm long, 5–6 mm thick, green with a red median stripe on each valve, and with red-based bulbous hairs. Seeds prismatic, 1.3–2 mm long, 1–1.5 mm thick. Complex heterozygote but mostly outcrossing. Gametic chromosome number, $n = 7$ (ring of 12 and 1 bivalent at meiotic metaphase I).

Type locality: Hungary, Ráhos near Budapest.

Distribution: North America, Old World, but not known as a native plant anywhere and probably of European origin from introduced North American taxa; in South America cultivated and sometimes naturalized.

Specimens examined:

BRAZIL. MINAS GERAIS: Distr. Carangola, trail from Arapongo to Fazenda de Grama, 1930, *Mexia 4232* (F, GH, UC). RIO DE JANEIRO: Villa Theresa, 1876, *Glaziou 8343* (C, NY, P). Between Prata and Albuquerque near Nova Friburgo, 1,000 m, 1965, *Pabst & Sick 10746* (HB). SÃO PAULO: Ubatuba, 1895, *Loefgren 11700* (SP). City of São Paulo, cult. Jard. da Comissão, *Edwall in 1896* (POM, SP). Botanical Garden of São Paulo, 1902, *Loefgren 11898*

(SP). Cultivated in fields of the Instituto Agronômia, *Souza in 1944* (SP-52168). PARANÁ: Cultivated in the garden of the Facultad de Farmácia in Curitiba, 1966, *Moreira & Joly 373* (US).

URUGUAY. MONTEVIDEO: Miguelito, *Fruchard in 1874* (P). Montevideo, *Arechavaleta in 1902* (POM).

ARGENTINA. BUENOS AIRES: Mar del Plata, near Arroyo "Las Chacras," 1932, *Gelsii 114* (POM). Pergamino, 1932, *Parodi 9977* (POM). Cultivated in the Botanical Garden of the Facultad de Agronomía, 1939, *Munz 15455* (GH, POM). Mar del Plata, 1954, *Calderón 363* (BAA).

ECUADOR. Near Cotocollas, 1885, *Sodíro 333* (F, GH, NY, POM). LOJA: Catacocha, 2,050 m, 1946, *Enspinosa 622* (RSA).

PERU. ANCASH: Huaráz, 2,600–2,650 m, 1949, *Proaño 5142* (P).

CHILE. Jahuel, in *1902* (HBG). Coast of Chile, 1920, *Claude-Joseph 1251* pro parte (US).

Although the name *O. glazioviana* Micheli (1882) antedates *O. erythrosepala* Borbas (1903), and we believe that these names refer to the same entity, as indicated by the synonymy above, I am not making the substitution at the present time pending further studies of *Oenothera* subsect. *Euoenothera*, which I hope will clarify the taxa involved. The type of *O. glazioviana* might alternatively be equivalent to *O. suaveolens* Pers. (1805).

49. **Oenothera villosa** Thunb., Prodr. Fl. Cap. 75. 1794.

A more complete treatment of this North American species, being reported for the first time as a naturalized plant in South America, has been given by Munz (1965: 135–136); see Dietrich & Raven (1976) for a discussion of the name.

49a. **Oenothera villosa** subsp. **strigosa** (Rydb.) Dietrich & Raven, Ann. Missouri Bot. Gard. 62: 382. 1976.

Onagra strigosa Rydb., Mem. New York Bot. Gard. 1: 278. 1900.
Oenothera strigosa (Rydb.) Mack & Bush, Fl. Jackson Co. Missouri 139. 1902; Munz, N. Amer. Fl., ser. 2, 5: 135. 1965.

Biennial herb, forming a rosette, erect, with a simple or branched main stem and side branches that arise sharply from the rosette, 5–20 dm tall. Plants densely strigillose, with an admixture of villous and glandular pubescence on the floral tube and the sepals. Rosette leaves very narrowly elliptic to narrowly oblanceolate, gradually narrower toward the petiole, 10–20 cm long, 2–5 cm wide; cauline leaves very narrowly elliptic to narrowly elliptic, acute, narrowly cuneate at the base, short-petiolate to sessile, 7–15 cm long, 1–2.5 cm wide; bracts narrowly elliptic to lanceolate, acute, attenuate to cuneate at the base, sessile to short-petiolate, 1–5 cm long, 0.5–1.2 cm wide; all leaves plane to crinkled at the margins, shallowly sinuate-denticulate. Inflorescence simple or branched. Floral tube 2–3.3 cm long. Buds lanceolate in outline, 1–1.8 cm long, 0.4–0.6 cm thick. Sepals 11–15 mm long, 3–5 mm wide; sepal tips 1–3 mm long. Petals very broadly obovate, 0.8–1.7 cm long, yellow. Anthers 4–7 mm long. Filaments 8–15 mm long. Style short, the anthers shedding pollen directly on the stigma at anthesis, 3–4.5 cm long. Stigma lobes 3–5 mm long. Ovary 10–15 mm long. Capsule narrowly lanceolate in outline, spreading from the stem at an acute angle, 1.8–4.5 cm long, 4–6 mm thick. Seeds prismatic, 1.5–2 mm long,

1–1.5 mm thick, dark brown. Self-pollinating complex heterozygote. Gametic chromosome number, $n = 7$ (ring of 14 at meiotic metaphase I).

Type: Locality unknown, Herb. Thunberg (S).

Distribution: Interior western United States and adjacent Canada. Naturalized at a few localities in the provinces of Córdoba, San Juan, and Mendoza, Argentina.

Specimens examined:

ARGENTINA. CÓRDOBA: Km 80 at Ruta 9, between Radio Nacional and Fabrica Postes de Cemento near Santa María, 1964, *Sublis 745* (CORD, MO). SAN JUAN: Calingasta, 1960, *Fabris & Marchionni 2391* (CTES, LP, M). Without definite locality, 1904, *Spegazzini 11274* (BAB). MENDOZA: Tupungato, 1933, *Ruiz Leal 1204* (Leal, POM). Dep. La Paz, Villa Pamonima, *Ruiz Leal in 1944* (Leal). Dep. Maipú, Las Barrancas, *Ruiz Leal in 1951* (Leal).

This species has not been reported previously from South America, although it is naturalized in several countries in Europe and in South Africa. The first collection from Argentina appears to be that of Spegazzini, cited above, made in 1904 in the province of San Juan; the species is apparently still not common. *Gaura parviflora* Dougl., another member of the Onagraceae from the Great Plains of North America, which resembles *O. villosa* in habit, is also present, apparently as an introduced plant, in Argentina, in the provinces of Córdoba and San Luis (Raven & Gregory, 1972). It was first collected in Argentina in 1876, and has spread to become much more common than *O. villosa.*

The widespread North American *Oenothera biennis* L., which is also abundantly naturalized in Europe, was collected once in a garden in Quilpué Prov. Valparaíso, Chile, by Lessauer in 1889 (M). It has apparently neither persisted nor spread, but it can easily be distinguished from *O. strigosa* by the lack of thick appressed strigulose pubescence, and more abundant glandular pubescence on the buds and in the inflorescence and its longer floral tubes (2.5 cm).

Excluded and Doubtful Names

Oenothera australis Salisb., Prodr. Stirp. 278: 1796. No authentic material seen. Type locality: Argentina, prov. Santa Cruz, Puerto Deseado (Porte Desire). Probably *O. odorata* Jacq.

O. crispa Schultes, Obs. Bot. 73. 1809. No authentic material seen.

O. erosa Lehm., Linnaea 3(2): Litt. 8. 1828. No authentic material seen.

O. guttata Molina, Saggio Sul. St. Nat. Chile. ed. 2: 134. 1810. According to Reiche & Philippi, Fl. Chile 261. 1898 = *Mimulus guttatus* Fisch. ex DC.

O. malacophylla Spach, Nouv. Ann. Mus. Hist. Nat. 4: 344. 1835. No authentic material seen.

Onothera mandoni H. Lév., Monde Pl. 8. 109: As plate opposite p. 48. 1898; Monogr. Onoth. 359. 1909; Bull. Acad. Int. Géogr. Bot. 19: 319. 1909, nom. illeg.

Oenothera micans Tausch, Flora 22: 559. 1839. No authentic material seen.

O. polymorpha H. Lév. race *mollissima* (L.) H. Lév. var. *arechaveletae* H. Lév., Monogr. Onoth. 365. 1909; Bull. Acad. Int. Géogr. Bot. 19: 325. 1909. No authentic material seen.

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WOOD ANATOMY OF ONAGRACEAE: ADDITIONAL SPECIES AND CONCEPTS[1]

Sherwin Carlquist[2]

Abstract

Wood anatomy of *Epilobium colchicum* subsp. *colchicum*, *Fuchsia excorticata*, and *Hauya heydeana* is described qualitatively and quantitatively. For the latter two species, large logs were available and wood portions from both inside and outside were analyzed. Although these three species offer no features new for Onagraceae, each adds features new for its respective genus. By means of numerical indices which are termed vulnerability and mesomorphy, respectively, values are presented to show the range in ecological characteristics of woods of the three species, as well as of all Onagraceae studied earlier. Onagraceae show a wide range in these indices and probably form a good model of what use indices in families with a broad ecological range will demonstrate. Wood from inside of logs of *Fuchsia excorticata* and *Hauya heydeana* is more xeromorphic than wood from the periphery.

In my monograph of wood anatomy of Onagraceae (Carlquist, 1975a), I attempted a sampling of woods based largely on availability of portions of suitable size. In any family in which herbs predominate, one is faced with arbitrary decisions as to whether some species which form little secondary xylem should be included. However, after the appearance of the monograph, Dr. Peter H. Raven placed at my disposal three wood samples with abundant secondary xylem for their respective genera, and otherwise of more than passing interest.

Materials and Methods

Epilobium colchicum Alboff subsp. *colchicum* (sect. *Chamaenerion*) was collected by Dr. Peter H. Raven from a streambed near the Lagodekhi Hotel in eastern Georgia, U.S.S.R., and is unusually woody for an *Epilobium*. The species of *Fuchsia* that forms perhaps the largest trees in that genus (and perhaps also in the family) is *F. excorticata* (J. R. & G. Forst.) L. f. A section from the base of a tree approximately 0.9 m in diameter (outline of section irregular) was supplied by the New Zealand Institute of Forestry. Dr. Dennis E. Breedlove's mesoamerican field work yielded a log, approximately 25 cm in diameter, of *Hauya heydeana* Donnell Smith. Because all the *Hauya* wood samples utilized in my earlier study were of *H. elegans* subsp. *cornuta*, material of the second species of this interesting genus was especially welcome. All three wood samples were dried. Methods of study were the same as those employed for dried samples in the earlier paper. Dr. Larry DeBuhr's work in preparing sections and macerations and in obtaining data is gratefully acknowledged. Because differences in wood anatomy were observed (Carlquist, 1975a) in samples of different diameter in *Hauya elegans* subsp. *cornuta*, both inner and outer portions of

[1] This study has been aided by a grant from the National Science Foundation, BMS 73-07055-A1. The wood of *Fuchsia excorticata* was provided by Dr. E. J. Godley, D.S.I.R., Christchurch, New Zealand.

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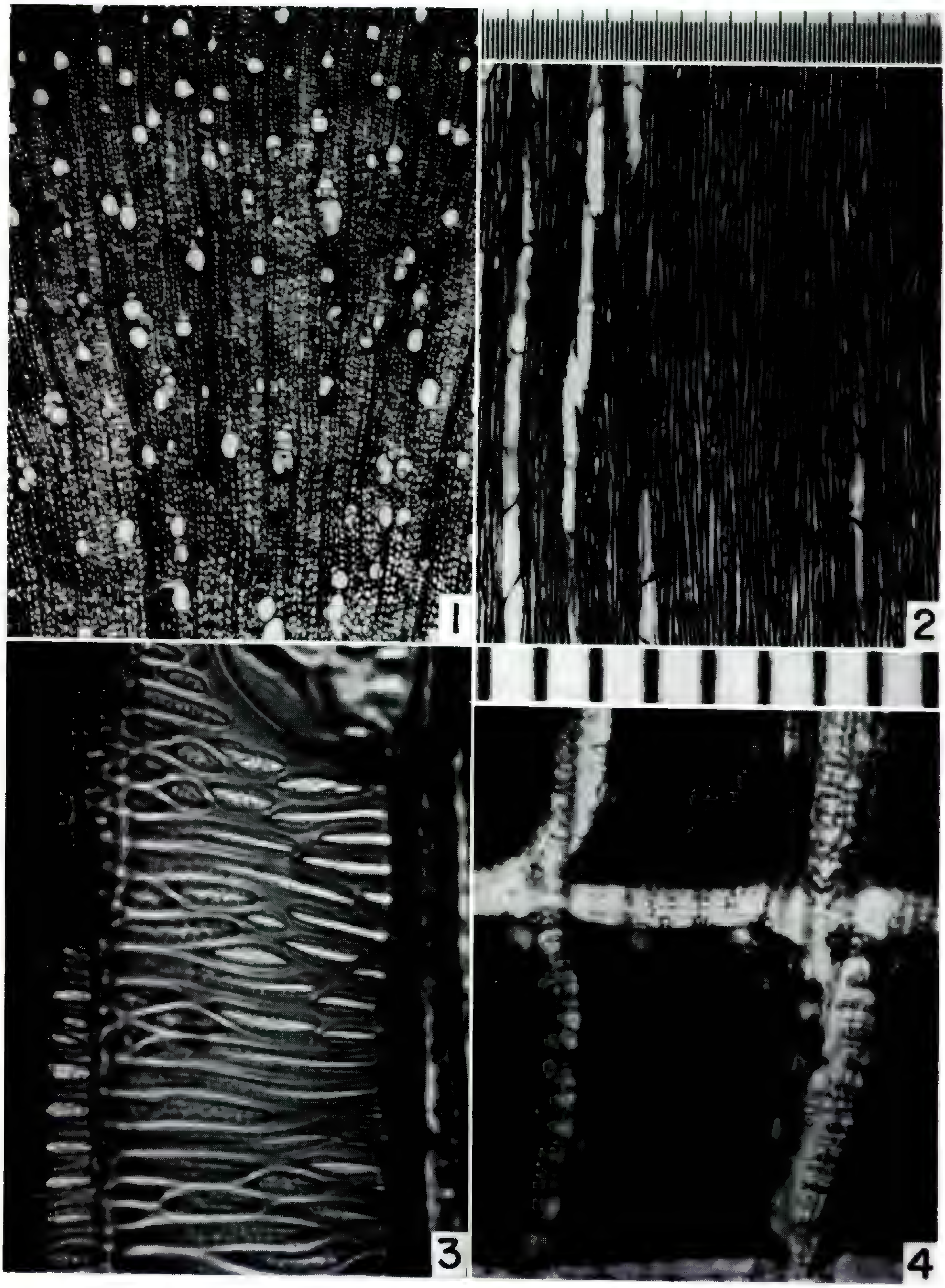


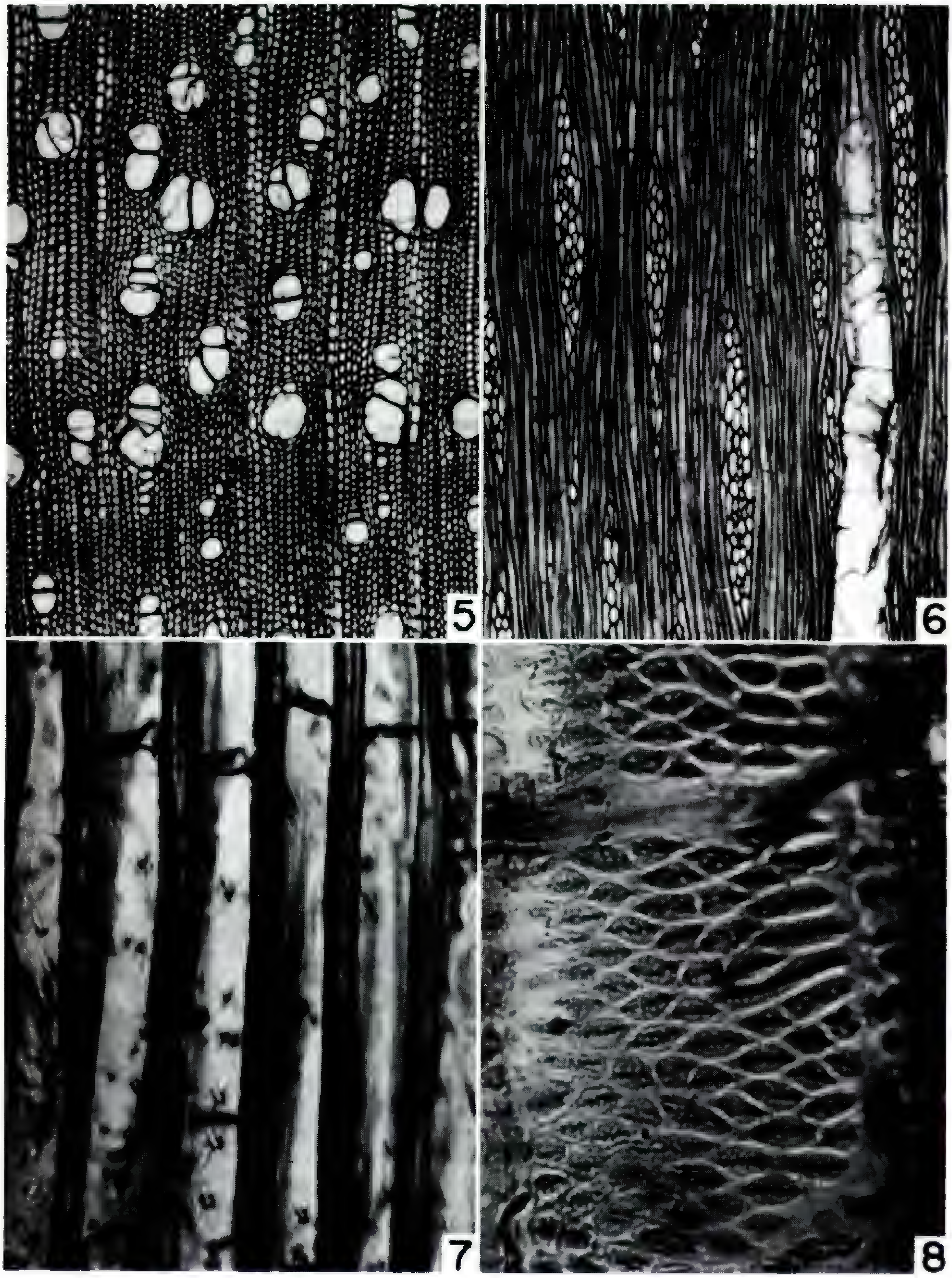
FIGURES 1–4. Wood sections of *Epilobium* and *Hauya*.—1–3. *Epilobium colchicum* Alboff subsp. *colchicum*, *Raven 26519* (MO).—1. Transection; parenchyma bands not shown in this photograph.—2. Tangential section; rays few, inconspicuous.—3. Portion of vessel wall from tangential section.—4. *Hauya heydeana* Donnell Smith, *Breedlove 15653* (MO). Radial section of ray cells showing nature of walls and starch grains embedded in dark-staining amorphous materials. [Magnification indicated by photograph of stage micrometer enlarged at same scale as applicable photomicrographs. Figs. 1–2, scale above Fig. 2 (finest divisions = 10 μm). Figs. 3–4, scale above Fig. 4 (divisions = 10 μm).]

the logs of *Fuchsia excorticata* and *Hauya heydeana* were studied. Quantitative data for both portions are reported below. Qualitative features of inner and outer portions are the same unless otherwise mentioned.

Anatomical Descriptions

Epilobium colchicum subsp. *colchicum*, *Raven 26519* (MO), Figs. 1–3. Growth rings present as parenchyma bands that are discontinuous in places around the stem. Mean vessel diameter, 50 μm; mean vessel element length, 184 μm. Vessels mostly solitary (Fig. 1); if grouped, in radial chains or multiples; mean number of vessels per group 1.36. Mean number of vessels per mm^2 of transection 38.1. Perforation plates simple. Lateral wall pitting of vessels basically alternate, appearing somewhat scalariform because pits are laterally elongate (Fig. 3). Pits conspicuously vestured (Fig. 3). Mean libriform fiber length 277 μm. Mean libriform fiber wall thickness 1.6 μm. Libriform fiber walls not gelatinous; pits simple. Axial parenchyma in the form of bands, with also a few vasicentric cells forming strands of one to three cells. Bands of axial parenchyma probably contain interxylary phloem, but determination uncertain because of lack of liquid preservation. Multiseriate rays more frequent than uniseriates, but both inconspicuous (Fig. 2) because upright cells predominate in multiseriates, with only a few square and procumbent cells. Uniseriate rays consist of upright cells only. Mean height of multiseriate rays 567 μm; uniseriates, 84 μm. Ray cells thin to moderately thick, the latter sometimes with bordered pits. No crystals observed. Amorphous deposits of dark-staining materials in some ray cells (Fig. 1). Wood not storied.

Fuchsia excorticata, Figs. 5–8. Growth rings inconspicuous in inner wood (Fig. 5), with narrower vessels in latewood, wider vessels in earlywood. Growth rings not evident in outer wood. Mean vessel diameter 73 μm in outer wood, 63 μm in inner wood. Mean vessel element length 325 μm in outer wood, 259 μm in inner wood. Vessels solitary or in multiples (Fig. 5), averaging 1.52 per group in outer wood, 1.76 per group in inner wood. Mean number of vessels per mm^2 of transection 32 in outer wood, 57 in inner wood. Perforation plates simple. Tyloses present in vessels, numerous, thin-walled (Fig. 6, right). Lateral wall pitting of vessels (Fig. 8) consists of alternate pits, angular and rhomboidal in outline or laterally elongate. Pits conspicuously vestured. Mean libriform fiber length 598 μm in outer wood, 562 μm in inner wood. Libriform fiber wall thickness 2.5 μm in outer wood, 2.9 μm in inner wood. Libriform fiber walls not noticeably gelatinous. Libriform fibers prominently septate (Fig. 7). Extremely minute vestiges of borders observed on pits of some libriform fibers (Fig. 7). Interxylary phloem absent. Axial parenchyma scanty vasicentric; strands consisting of three to five cells per strand. Rays predominantly multiseriate (Fig. 6); uniseriates infrequent, virtually absent in inner wood. Mean multiseriate ray height 755 μm in outer wood, 494 μm in inner wood; uniseriates (outer wood), 224 μm. Multiseriates composed of upright, square and procumbent cells. Uniseriates composed wholly of erect cells. No crystals observed. A few ray cells with dark-staining contents (Fig. 6). Wood not storied.



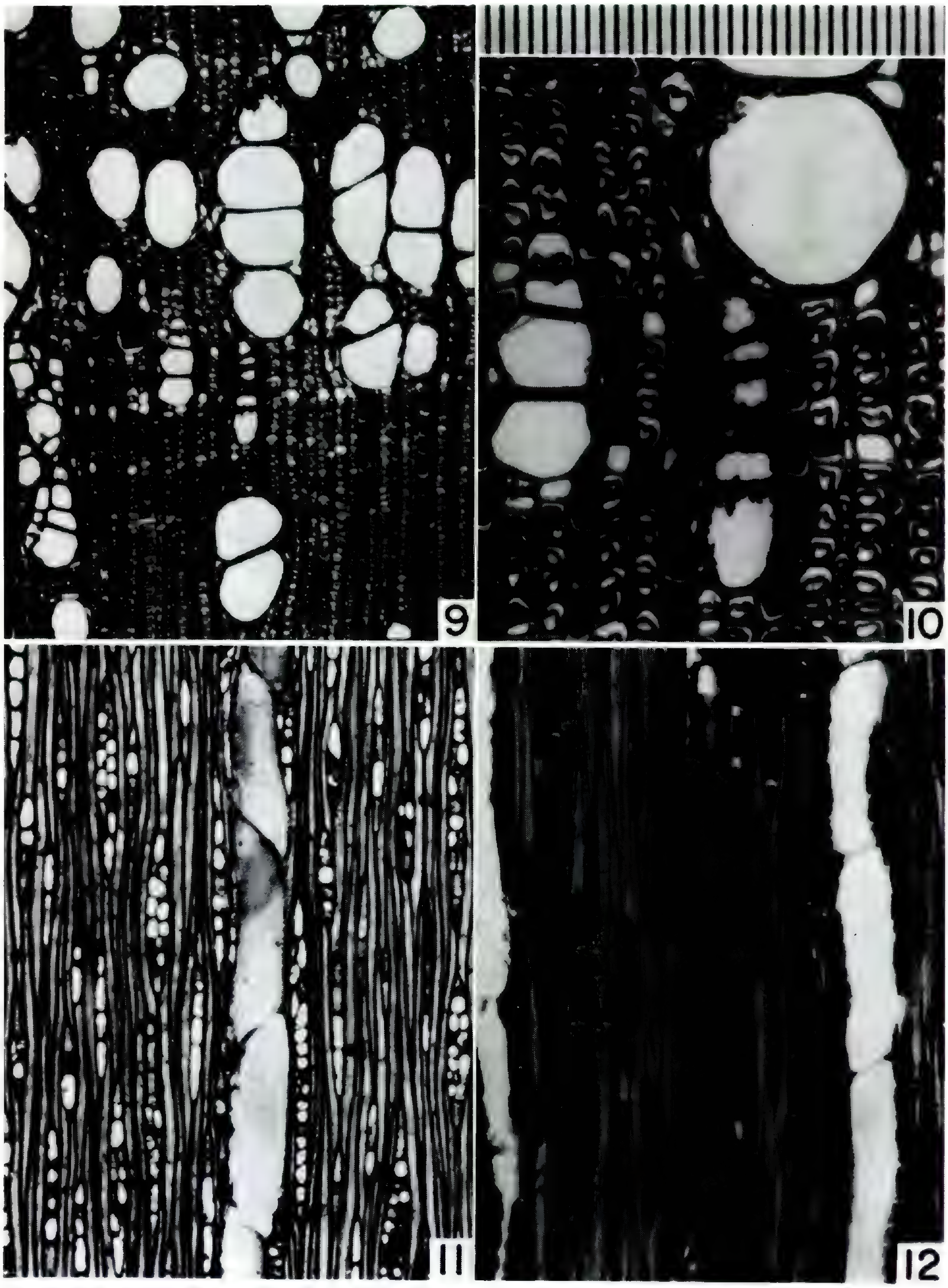
FIGURES 5–8. Wood sections of *Fuchsia excorticata* (J. R. & G. Forst.) L. f., collected by the New Zealand Forestry Institute.—5. Transection, from near center of large log.—6. Tangential section, from near periphery of large log.—7. Septate fibers, showing pitting, from radial section.—8. Vessel wall from radial section, showing vestured pits, angular in outline, some laterally elongate. [Magnification for Figs. 5–6, shown above Fig. 2. Scale for Figs. 7–8, shown above Fig. 4.]

Hauya heydeana, Breedlove 15653 (MO), Figs. 4, 9–12. Growth rings inconspicuous, vessels wider in earlywood (Fig. 9). Mean vessel diameter 111 μm in outer wood, 80 μm in inner wood. Mean vessel element length 506 μm in outer wood, 481 μm in inner wood. Vessels mostly grouped in short radial chains (Fig. 9), 2.52 per group in outer wood, 2.24 in inner wood. Mean number of vessels per mm^2 of transection 31 in outer wood, 56 in inner wood. Perforation plates simple. Lateral wall pitting of vessels alternate, pits round in outline with some tendency toward laterally elongate pits. Vesturing on pits not readily visible. Mean length of libriform fibers 874 μm in outer wood, 903 μm in inner wood. Mean libriform fiber wall thickness 2.5 μm in outer wood, 2.0 μm in inner wood. Libriform fibers with inner portion of wall markedly gelatinous (Fig. 10). Axial parenchyma mostly vasicentric, but with some cells in tangential bands (Figs. 9, 10, 12), as in *H. elegans* subsp. *cornuta*; parenchyma cells consist of two or three cells per strand. No interxylary phloem present. Both multiseriate and uniseriate rays present (Figs. 11–12). Mean multiseriate ray height 497 μm in outer wood, 609 μm in inner wood. Mean uniseriate ray height 352 μm in outer wood, 305 μm in inner wood. Both multiseriate and uniseriate rays consisting of upright, square and procumbent cells. Ray cell walls thick (Fig. 4), some with bordered pits. Massive deposits of dark-staining materials in ray cells and axial parenchyma (Figs. 4, 9–10, 12). Starch grains also present in ray cells (Fig. 4) and axial parenchyma cells. Wood not storied.

Comparisons

Epilobium colchicum (sect. *Chamaenerion*), a woody perennial, differs from *E. paniculatum* (sect. *Xerolobium*), a rank annual, most notably in the presence of axial parenchyma bands (Carlquist, 1975a). Phloem is presumptively present in these bands. Because these bands do not extend all the way around the stem, the apparent absence of cork cells, such as reported by Moss (1936) in *Epilobium angustifolium* (also of sect. *Chamaenerion*), is understandable. *Epilobium colchicum* shows laterally widened pits on the vessel walls (Fig. 3) with exceptional clarity. These pits are very clearly vestured. Species of the tribe Epilobieae do not, in wideness of vessels, length of vessel elements, and low number of vessels per mm^2 of transection, approach the two species of *Hauya*. Still, one may note that *E. colchicum* has the most mesomorphic woods of the three species of Epilobieae now studied. In view of its riparian habitat, which contrasts strongly with the xeric habitats of the other two species, this correlation is logical.

Fuchsia excorticata falls within the range of wood features reported for *Fuchsia* earlier. Scanning electron micrographs of the vestured pits of *F. excorticata* have been presented by Butterfield & Meylan (1973). The potential interest of *F. excorticata* in relation to wood anatomy of Onagraceae is whether, with trunks of such large size, changes in quantitative characteristics occur with age. As the above descriptions indicate, some changes do occur. Vessel elements are appreciably wider, longer, and few per mm^2 in the outer wood than in the inner wood. Libriform fibers are longer and slightly more thin-walled in the outer wood. Multiseriate rays are taller in the outer wood. Although ray histology



FIGURES 9–12. Wood sections from periphery of log of *Hauya heydeana* Donnell Smith, *Breedlove 15653* (MO).—9. Transection, showing a growth ring.—10. Transection, enlarged, showing gelatinous walls of libriform fibers, dark-staining contents of parenchyma cells, and distribution of axial parenchyma.—11. Tangential section, showing nature of rays.—12. Another tangential section, showing massive deposits of gummy materials in rays, axial parenchyma. [Scale for Figs. 9, 11–12, shown above Fig. 2. Scale for Fig. 10 above Fig. 10.]

does not seem to change, there is a change in presence of uniseriate rays. In the outer wood of *F. excorticata* (Fig. 6), uniseriates are present, whereas they can be said to be virtually absent in the inner wood. This is exceptional in *Fuchsia*, although in most species studied, multiseriates do predominate over uniseriates (Carlquist, 1975a). The quantitative changes with age are in accordance with those one expects in a typical woody dicotyledon (Bailey & Tupper, 1918; Carlquist, 1975b).

Hauya heydeana differs in some features of wood anatomy from the species studied previously, *H. elegans* subsp. *cornuta*. Most notable are the ergastic materials. Whereas *H. elegans* subsp. *cornuta* had, in all collections, large crystals within fibriform cells (sometimes with smaller crystals), no crystals of any sort could be detected in any of the sections of *H. heydeana*. On the other hand, wood of *H. heydeana* is dark in color, a fact undoubtedly related to the abundance of dark-staining deposits in ray and axial parenchyma cells, as revealed by the photomicrographs (Figs. 4, 9–10, 12). The presence of thick-walled ray cells with bordered pits (Fig. 4) is to be expected in view of the occurrence of this phenomenon in *H. elegans* subsp. *cornuta*, *Camissonia crassifolia*, and *Epilobium colchicum* subsp. *colchicum*. The occurrence of axial parenchyma cell groups in *H. heydeana* (Fig. 10) is much like that in *H. elegans* subsp. *cornuta*, and emphasizes the generic distinctness of *Hauya*. Ray histology does not appear to change appreciably with age in *H. heydeana*, although such large trunks as those of *H. elegans* subsp. *cornuta* were not available, perhaps because this species does not form as large trees. The presence of starch in ray cells of *H. heydeana* (Fig. 4), conspicuously preserved because of embedding of the starch grains in the amorphous deposits, is to be expected for Onagraceae as a whole and was also observed in *H. elegans* subsp. *cornuta*. The two species are alike in the absence of septa in fibers, absence of interxylary phloem, and absence of tyloses. The gelatinous fibers of *H. heydeana* (Fig. 10) differ from the non-gelatinous ones in *H. elegans* subsp. *cornuta*, although gelatinous fibers are very common in Onagraceae (Carlquist, 1975a). Pits on vessels of *H. heydeana* are probably vestured, but that vesturing is so fine that it appears only as a slight darkening of the edge of the pit aperture; scanning electron microscopy would be required for definitive demonstration.

Qualitatively, wood characteristics of *H. heydeana* are much like those of *H. elegans* subsp. *cornuta*, indicating an equally mesomorphic conducting system conformation. The changes from inside to outside of a log of *H. heydeana* in quantitative features are much like those of *H. elegans* subsp. *cornuta* or *Fuchsia excorticata*: vessels elements are wider, longer, and fewer per mm^2 of transection in the outer wood. Rays are shorter in the outer wood of both species of *Hauya*, contrary to the increase in ray height in *Fuchsia excorticata*.

Ecological Concepts

In my survey of Onagraceae (Carlquist, 1975a), I used, for groupings of species, an index based upon the sum of mean vessel diameter and mean vessel element length. That index appeared to reflect accurately the ecology of onagra-

Table 1. Ecological indices for woods of Onagraceae.

Species	V	M
Fuchsieae		
Fuchsia boliviana Britton	1.54	559
F. cyrtandroides J. W. Moore	5.15	2,260
F. excorticata (J. R. & G. Forst.) L. f.		
inside	1.08	280
outside	2.28	741
F. fulgens DC.	1.67	499
F. magellanica Lam. var. *globosa* (Lindl.) Bailey	1.75	673
F. magellanica var. *macrostemma* (Ruiz & Pavón) Munz	1.39	489
F. paniculata Lindl.	3.91	2,151
F. parviflora Lindl.	0.52	245
F. splendens Zucc.	1.28	591
F. tincta I. M. Johnston	1.08	356
F. tuberosa Krause	0.22	71
All Fuchsieae	1.99	634
Lopezieae		
Lopezia grandiflora Zucc.	1.17	579
L. langmaniae Miranda	2.07	797
L. longiflora (Decne.) Plitmann, Raven & Breedlove	5.79	1,847
L. lopezioides (H. & A.) Plitmann, Raven & Breedlove, *Breedlove 7268*	2.00	902
L. lopezioides, Breedlove 8052	2.96	929
L. miniata Lag. ex DC. subsp. *miniata*	0.63	187
L. miniata subsp. *paniculata* (Seem.) Plitmann, Raven & Breedlove	1.21	439
L. racemosa Cav. subsp. *moelchenensis* Plitmann, Raven & Breedlove	0.32	86
L. racemosa subsp. *racemosa*	0.86	237
L. riesenbachia Plitmann, Raven & Breedlove	0.46	155
L. semeiandra Plitmann, Raven & Breedlove	3.68	1,417
Lopezieae: shrubs combined	2.70	961
Lopezieae: annuals, suffrutescent perennials combined	0.67	215
Onagreae		
Calylophus hartwegii (Benth.) Raven subsp. *pubescens* (A. Gray) Towner & Raven	0.14	26
C. serrulatus (Nutt.) Raven	0.13	18
Camissonia californica Raven	0.76	234
C. crassifolia (Greene) Raven	0.12	25
C. cheiranthifolia (Hornem. ex Spreng.) Raimann	0.41	68
C. megalantha (Munz) Raven	0.83	338
Clarkia xantiana A. Gray	0.35	119
Gaura biennis L.	0.66	174
G. longiflora Spach	1.10	375
G. parviflora Dougl.	1.13	267
G. sinuata Nutt. ex Sér.	0.14	15
G. villosa Torr. subsp. *villosa*	0.52	134
Gongylocarpus fruticulosus (Benth.) Brandegee subsp. *glaber* (Thomas) Carlquist & Raven	0.53	120
G. rubricaulis Schlecht. & Cham.	0.75	271
Heterogaura heterandra (Torr.) Cov.	0.69	197
Oenothera deltoides Torr. & Frém. subsp. *howellii* (Munz) Klein	0.81	237
O. drummondii Hooker	0.74	169
O. elata H.B.K.	1.19	353
O. linifolia Nutt.	0.20	48
Xylonagra arborea (Kell.) Donnell Smith & Rose subsp. *wigginsii* Munz	1.68	314
Onagreae: annuals combined	0.54	161
Onagreae: caudex perennials	0.22	48

TABLE 1. (continued)

Species	V	M
Jussiaeeae		
Ludwigia octovalvis (Jacq.) Raven, *Raven 6571*	0.73	313
L. octovalvis, *Raven 18670*	0.67	287
L. uruguayensis (Cambess.) Hara	1.54	548
Epilobieae		
Epilobium colchicum Alboff subsp. *colchicum*	1.32	242
E. paniculatum Nutt. ex Torr. & A. Gray	0.52	122
E. (*Zauschneria*) *canum* subsp. *canum*	0.11	17
Hauyeae		
Hauya elegans DC. subsp. *cornuta* (Hemsley) Raven & Breedlove, *Breedlove 6432*	3.20	1,328
H. elegans subsp. *cornuta*, *Breedlove 10589*	3.38	1,153
H. elegans subsp. *cornuta*, *Carlquist VI-1958*	2.96	1,270
Hauya heydeana Donnell Smith		
inside	1.43	688
outside	3.50	1,771
Hauyeae combined:	2.89	1,242

ceous species and species groups. More recently (Carlquist, 1977; Carlquist & DeBuhr, 1977) I have constructed additional indices for wood ecology. One of these, which may be termed "vulnerability" (V in Table 1) consists of the mean vessel diameter divided by the mean number of vessels per mm^2 of transection. Although vessel diameter and number of vessels per mm^2 are roughly inversely proportional for mesophytes (Carlquist, 1975b: 183), xerophytes tend to have narrower vessels and more numerous vessels per mm^2 than would be expected on the basis of study of mesomorphic woods only, as shown by the desert shrubs included in the graph just cited. This "redundancy" of vessels in xerophytes provides a conductive tissue in which a large number of vessels could be disabled by air embolisms without appreciably lessening conductive capacity. Thus a low value for "vulnerability" can be construed as a high degree of "safety" under water stress conditions and, therefore, xeromorphy.

Vessel element length seems a sensitive indication of xeromorphy or mesomorphy (Carlquist, 1975b). Although one could argue that vessel diameter and number of vessels per mm^2 are somewhat interrelated, vessel element length is controlled entirely independently, by length of fusiform cambial initials. Long vessel elements can be hypothesized to occur in mesomorphic conductive systems, short ones in xeromorphic woods. Therefore, multiplying the "vulnerability" index by mean vessel element length yields a figure which is termed "mesomorphy" (M in Table 1) here. The higher the value of this value, the greater the hypothetical mesomorphy of the wood. The family Penaeaceae illustrated that this index is reliable on the basis of known species (Carlquist & DeBuhr, 1977). It also appears to be reliable in Onagraceae. Because Onagraceae occupy a notably wide range of ecological situations, I am presenting here the two indices for all species of Onagraceae studied to date (Table 1).

One can interpret these indices only within ranges. A "V" figure markedly

below 1.0 (perhaps 0.1–0.5) would indicate a high degree of xeromorphy (Carlquist, 1977), and the lower limit for true mesomorphy would be close to 3.0.

With respect to the "M" index, true xeromorphy is indicated probably by a level below 30.0. In Tremandraceae, values range between 15.4 and 45.0 (Carlquist, 1977), and the highest "M" value in Penaeaceae was 587 (Carlquist & DeBuhr, 1977). Small sampling differences can alter values of these indices, obviously. Future development of these indices will indicate their potential validity in ecological and physiological analyses of dicotyledon families. However, the V and M indices show the same sequence (Hauyeae; Fuchsieae; large shrubby Lopezieae; annual or suffrutescent Lopezieae; annual Onagreae; perennial Onagreae) as was demonstrated by the vessel diameter + vessel element length figure (Carlquist, 1975a). The latter figure, however, was higher for the Jussieeae than for Hauyeae, a fact I related to the hydrophytic habit of Jussieeae. However, the V value for Jussieeae is low, which one might not expect in a hydrophyte. Perhaps the fact that Jussieeae grow in seasonally wet but often drying environments explains why they have xylem that combines low vulnerability with mesomorphy. A relatively high amount of redundancy in vessels in Jussieeae would cope well with the drying out of habitats. The high V value for Hauyeae (and, to a lesser extent, Fuchsieae) would correlate with lack of any marked water stress in the habitats of these species.

If one can interpret the M value for inside wood versus outer wood in a log, *Fuchsia excorticata* and both species of *Hauya* begin with appreciably less mesomorphic wood structure and increase in mesomorphy, as well as vulnerability, with age. This would not be unexpected in view of my earlier (1975b) considerations. However, if this phenomenon does prove to be widespread in dicotyledons, we must conclude that vascular plants tend to have less vulnerability, less mesomorphy in earlier-formed xylem. If the root system of a woody dicotyledon would be expected to experience more severe fluctuation in water availability (nearer the soil surface) than when a tree is older, this would be logical. However, study of additional species would be valuable in this respect. Future application of these indices will indicate their potential validity in physiological analyses of dicotyledon families. Onagraceae is, however, a critical family in this respect, and appears to reflect the broad range of ecology of the family as a whole, and the ecology of individual species and of growth forms, as discussed earlier (1975a) and here.

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A NEW SPECIES OF *LOPEZIA* (ONAGRACEAE) FROM SINALOA, MEXICO[1]

PETER H. RAVEN[2]

ABSTRACT

Lopezia concinna Raven is described from Sinaloa, Mexico. It is unique in the genus in its elaborately marked petals and wide lower sepals. It appears to be closely related to *L. conjungens*. See p. 641.

Within the largely Mexican genus *Lopezia*, the evolution of distinctive annual taxa at the relatively arid margins of the range is a pronounced trend (Plitmann et al., 1973; Plitmann et al., 1975). Within sect. *Lopezia*, a group of nine species, three such annual derivatives—*L. cornuta* S. Wats., *L. ciliatula* Plitmann, Raven & Breedlove, and *L. conjungens* T. S. Brandegee—occur within the state of Sinaloa, and the latter two are restricted to it. Nevertheless, the discovery of a distinctive and very handsome novelty within this group by James L. Reveal and Raymond M. Harley, to whom I am most grateful for the privilege of studying their material, is of considerable interest, and suggests the possibility of further additions to this genus, which now totals 22 species.

Lopezia (sect. Lopezia) **concinna** Raven, sp. nov.—FIGS. 1–2.

Species sepalis dimorphis 10–13 mm longis, petalis superioribus 14–16 mm longis ornate notatis eglandulosis ab aliis sectionis *Lopeziae* diversa.

Erect *annual. Stems* 3–7 dm tall, well branched, terete, reddish, hirsute with white hairs. *Leaves* 2.5–5.7 cm long, 1.4–2.5 cm wide, ovate, truncate or rounded at the base, acute or acuminate at the apex, subentire or shallowly serrulate-crenulate, subglabrous or with a few scattered hairs along the midrib below and along the margins, with 5–8 veins on each side of the midrib, mostly subopposite; petioles 8–30 cm long, hirsute. *Pedicels* 10–14 mm long, spreading, glabrous. *Sepals* 10–13 mm long, the upper three 1–1.5 mm wide, linear and keeled at the apex, the single lower one 3–3.5 mm wide and lanceolate, keeled along its entire length. *Lower petals* 11–14 mm long, 6–7.5 mm wide, subovate, entire, clawed, the claw 2–3 mm long, the petals entirely fuchsia purple with a dark spot at junction of the claw; upper petals 14–16 mm long, 1.5–2 mm wide, linear, shortly clawed, subacute at the apex, slightly auriculate at the base, fuchsia purple with a narrow V-shaped dark stripe, a parallel white stripe, then a thick parallel orange stripe, a broad parallel white stripe, and a final ornate dark stripe in the third of the limb just about the auricles; glands absent, but the flower evidently nectariferous. *Fertile stamen* 8–9.3 mm long; filament com-

[1] Support from the U. S. National Science Foundation is gratefully acknowledged. Peter Hoch provided valuable technical assistance, Steven R. Seavey the chromosomal information, and Richard H. Eyde comments on the floral anatomy. The herbarium of the University of California, Berkeley (UC), kindly loaned the type and only known specimen of *Lopezia conjungens*.

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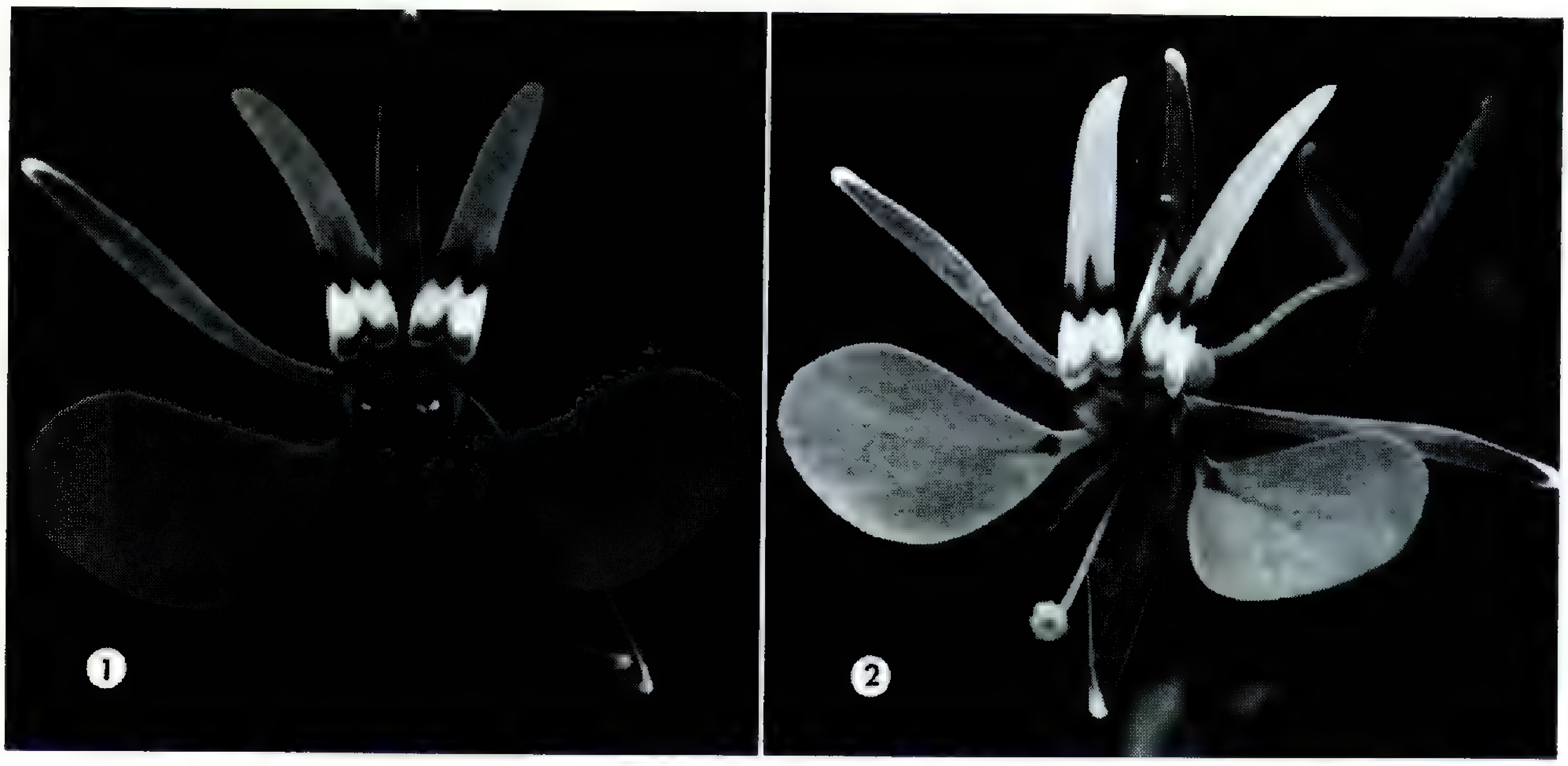


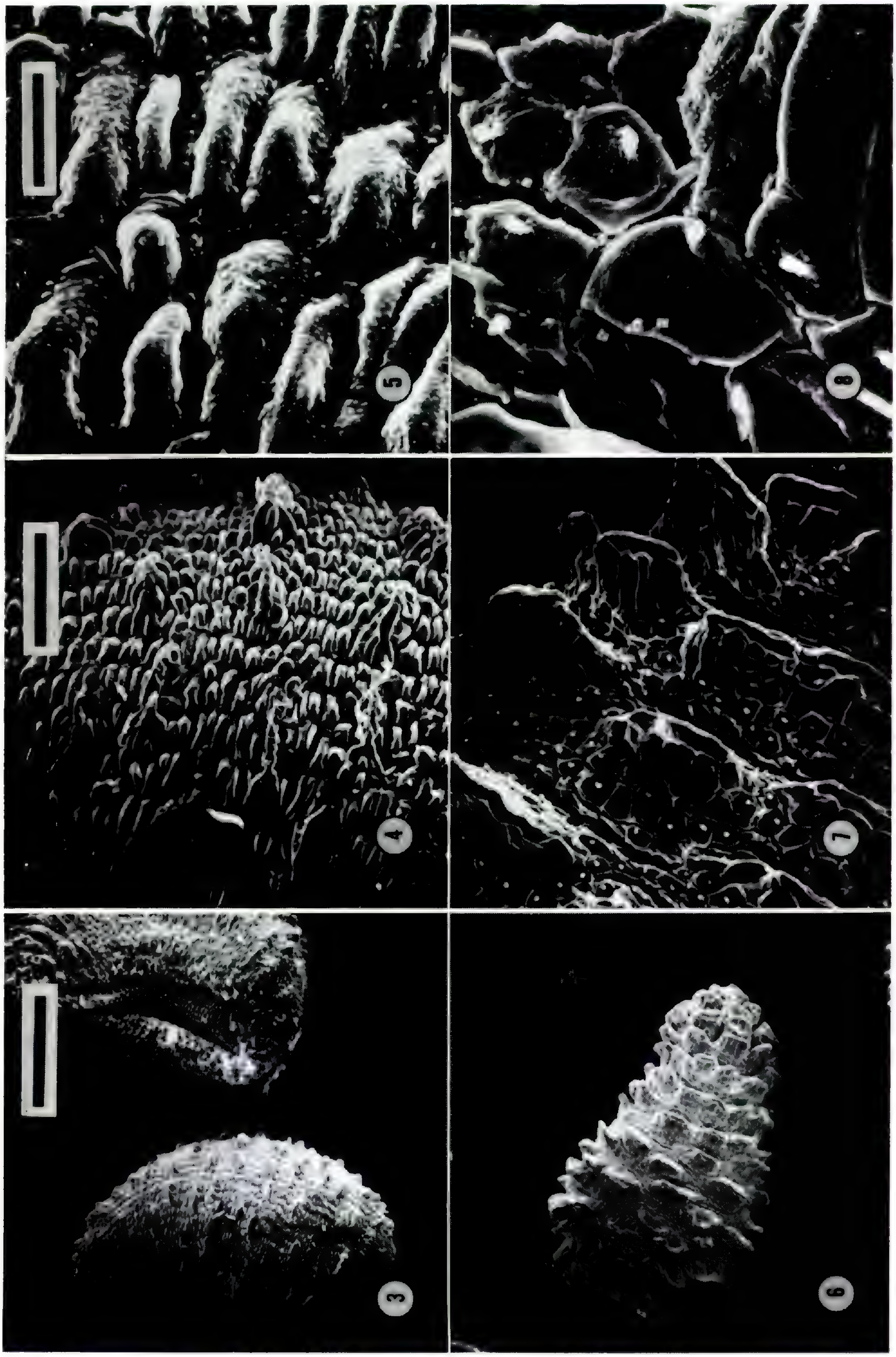
FIGURES 1–2. Flowers of *Lopezia concinna* Raven, × 2.7; photographs by Robert Srenco. —1. Before explosive release of the fertile stamen by the staminode. Note drops of nectar at the base of the upper petals.—2. After release of the fertile stamen. The staminode has curved downward, the fertile stamen upward, and the style elongated, carrying the stigma into the position formerly occupied by the staminode holding the fertile stamen under tension.

pressed, 6–7 mm long, 0.8–1.2 mm wide, dark red at the base, shading to pink at the point of anther attachment; anther 2–2.5 mm long, 0.2–0.3 mm wide, ruby red. *Staminode* 8–9.5 mm long, suborbicular or obovate-spatulate, retuse at the apex, abruptly narrowed to a claw 4–4.5 mm long, ruby red, the claw pink. *Style* 8–10 mm long, pink; stigma 1.4–1.6 mm in diameter, white. *Ovary* broadly ellipsoid to rotund, 2.5–4 mm long, 2–3.2 mm wide, glabrous. *Capsule* 6–7 mm long, 3.5–4.5 mm thick, obovoid-elongate, fleshy. *Seeds* several in each locule, 1.3–1.6 mm long, oblong-ovoid, uncurved, with transverse protuberances over the entire surface, brown. Gametic chromosome number, $n = 10$ (10 bivalents at meiotic metaphase I).

TYPE: MEXICO. SINALOA: Along the dirt road from Rosario to Plomosas, about 3.5 km east of La Rastra and 3.2 km up the grade from a river crossing, this about 1.5 km south of Rosario, on a rocky road cut along the steep canyon wall, 8 Oct. 1975, *James L. Reveal & Raymond M. Harley 4064* (MO-2412198, holotype; CAS, IPN, K, MEXU, MICH, US, isotypes).

Distribution: Known only from the type collection. See p. 641.

This elegant new species, with its beautiful flowers (Figs. 1–2), differs from all other members of its section, except *L. conjungens*, in its lack of glands on the upper petals. That species is also known only from its type collection, and we have been unable to examine living material. Its type and only known locality is some 270 km northwest of the locality in southernmost Sinaloa where *L. concinna* was discovered. The only known plants of *L. conjungens* are subglabrous, have much smaller and paler flowers, and lack the elaborate markings of the petals of *L. concinna*. Indeed, the markings in the petals of *L. concinna* and its conspicuously wider lower sepal are absolutely distinctive within the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genus. Its flowers are substantially larger than those of all other species of the section except for those of the very different *L. suffrutescens* Munz. The seeds of the two species (Figs. 3–8) both have transverse ridges, but those of *L. concinna* are much coarser and occupy the entire surface of the seed, whereas those of *L. conjungens* are fine and widely spaced. The epidermal cells on the seeds of *L. conjungens* are oblong, while those on the seeds of *L. concinna* more nearly square. Finally, the seeds of *L. conjungens* are more markedly incurved than those of *L. concinna.* More material of each species, and especially living material of *L. conjungens,* will be necessary to clarify their relationships, which appear close; further, the two species may well have been derived from a common ancestor, or *L. concinna* may have given rise to *L. conjungens.*

We have not observed nectar production, which is copious in *L. concinna* and apparently arises from the base of the petals, in any other species of sect. *Lopezia.* Richard H. Eyde sectioned floral material of *L. concinna,* from progeny of the type grown at the Missouri Botanical Garden, and found the order of divergence of the parts to be as reported for *L. hintonii* Foster [= *L. miniata* Lag. ex DC. subsp. *hintonii* (Foster) Plitmann, Raven & Breedlove] by Eyde & Morgan (1973), with nectaries in the usual position for *Lopezia.*

The chromosome number was determined in progeny of the type collection grown in the experimental greenhouse at the Missouri Botanical Garden. Details of the flowers have also been studied in this cultivated material.

At its type and only known locality, *L. concinna* was relatively common in protected, dripping wet recesses along a north-facing cliff-face in a forest dominated by trees of *Bursera* with *Hyptis, Salvia, Polymnia, Lasiacis, Malvaviscus,* and *Euphorbia* subg. *Poinsettia* common in the understory. Directly associated with the plants of the *Lopezia* were *Amemia affinis* Baker, *Cuphea llavea* Lex., *Peperomia* sp., *Pinguicula crenatiloba* DC., *Polypodium pumila* (Bonpl.) Cogn., *Pterolepis pumila* (Bonpl.) Cogn., and *Salvia misella* Kunth.

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Note added in proof

While this article was in press, D. E. Breedlove kindly sent a second collection of the new species from 80 km farther east: Durango, canyon of Río Mezquital near Nayarit, ca. 750 m, 1–6 Nov. 1977, *G. H. Bolton* 101 (CAS, MO).

←

Figures 3–8. Scanning electron micrographs of seeds of two closely related species of *Lopezia* sect. *Lopezia.* All from the respective type specimens. The bars at the top of the plate indicate, respectively, 0.5 μm, 125 μm, and 25 μm.—3–5. *L. conjungens.*—6–8. *L. concinna.*

REINTERPRETATION OF THE TYPE OF *GODETIA BOTTAE* SPACH (ONAGRACEAE)[1]

Peter H. Raven[2] and Dennis R. Parnell[3]

Paolo Emilio Botta, who traveled in the *Héros*, commanded by August Bernard Duhaut-Cilly, collected birds and plants along the coast of California in 1827 and 1828 (McKelvey, 1955). One of these was the type of the taxon later described as *Godetia bottae* Spach (1835). It is preserved in the Herbarium of the Muséum National d'Histoire Naturelle, Paris (P), and is annotated in Édouard Spach's hand, "Godetia Bottae, nob. (Spach, 1839), California, M. Botta." A second specimen is annotated simply "Godetia bottae" with an inscription in another hand that says "Monterey, M. P. E. Botta, 1829." According to Dr. A. Lourteig, this second hand is that of Botta.

At any rate, these specimens are not the species that has subsequently come to be known as *Clarkia bottae* (Spach) Lewis & Lewis (1955), but rather the one known as *C. deflexa* (Jeps.) Lewis & Lewis. Harlan Lewis concurs in this redetermination. Judged from the ports that the *Héros* visited regularly and the time of year, they were probably collected in the summer of 1827 or that of 1828 either at Santa Barbara or at San Pedro; the species does not occur at or near Monterey and the notation on the second herbarium specimen must have been made in error. Collections from Monterey County assigned by Lewis & Lewis (1955) to the taxon *C. deflexa* have been shown to comprise a distinct species described as *C. jolonensis* Parnell (1970).

In view of these findings, the following new synonymy is appropriate:

Clarkia (subsectio *Peripetasma* Lewis & Lewis) **lewisii** Raven & Parnell, sp. nov.

Clarkia bottae sensu Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 315. 1955; non *Godetia bottae* Spach, Nouv. Ann. Mus. Hist. Nat. 4: 393. 1835.

A *C. cylindrico* differt: tubo floralis annulo pilorum summo intus, 1.5–3 mm longus, non colorato intus.

Type: U.S.A. california: Monterey Co., Point Lobos, along the trail to China Cove from the end of the road, 26 June 1947, *H.* and *M. Lewis 498* (LA).

This species is dedicated to Harlan Lewis of the University of California, Los Angeles, who has made *Clarkia* one of the groups that has contributed most to our understanding of plant evolution. As two of his former graduate students, we feel a sincere debt of gratitude to him.

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[1] Support from the U. S. National Science Foundation through grants to Peter Raven is gratefully acknowledged. Dr. A. Lourteig and Professor Harlan Lewis have helped us in the interpretation of the specimens discussed herein.

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Ann. Missouri Bot. Gard. 64: 642–643. 1977.

Clarkia bottae (Spach) Lewis & Lewis, Madroño 12: 33. 1953.

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Oenothera bottae (Spach) Torr. & A. Gray, Fl. N. Amer. 1: 505. 1840.
Oenothera godetia Steud., Nom. Bot. ed. 2, 2: 206. 1841, illeg. subs.
Godetia deflexa Jeps., Univ. Calif. Publ. Bot. 2: 332. 1907.
Godetia bottae Spach var. *deflexa* (Jeps.) Hitchc., Bot. Gaz. (Crawfordsville) 89: 355. 1930.
Clarkia deflexa (Jeps.) Lewis & Lewis, Madroño 12: 33. 1953; Lewis & Lewis, Univ. Calif. Publ. Bot. 20: 334. 1955.

With the description of *Clarkia jolonensis* Parnell (1970) and *C. rostrata* Davis (1970), the number of species of sect. *Peripetasma* Lewis & Lewis is now 11.

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REPRODUCTIVE STRUCTURES AND EVOLUTION IN LUDWIGIA (ONAGRACEAE). I. ANDROECIUM, PLACENTATION, MERISM[1]

Richard H. Eyde[2]

Abstract

This article, based on serial sections from 19 species of *Ludwigia* (supplemented where necessary with preparations from other Onagraceae), begins an effort to outline the evolution of flower, fruit, and seed characters within the genus and to link the outline with what is known of floral evolution elsewhere in the family. New observations include the following: all *Ludwigia* anthers have a prominent endothecium, and developing anthers of certain advanced species are markedly H-shaped in cross section; pollen of two species matures in isolated packets; ovules of *L. leptocarpa*, though commonly 1-seriate, can be distally pluriseriate; only rarely does a *Ludwigia* placenta have a median groove suggesting paired carpel margins. The deeply intrusive placentas seen in section *Myrtocarpus*, but lacking in some of the other sections, are probably ancestral, and the old idea that diplostemony and 4+-mery are ancestral holds up well when reexamined critically.

Few families have been as intensively studied by evolutionary botanists as the Onagraceae. Relationships among many infraspecific variants and among closely connected species groups have been firmly established through cytological work, breeding experiments, and field observations of reproductive events. As one proceeds to more widely separated taxa, however, biosystematic methods become inapplicable; consequently, evolutionary links among the genera of Onagraceae are not yet well understood. Structural comparison remains the best—perhaps the only—way to improve our knowledge of these links. First, structural differences among the taxa must be identified, then the direction of evolutionary change can be inferred by critically weighing the alternatives.

The Onagraceae are ideal in several respects for comparative studies of floral structure. For one thing, the family is of manageable size: Raven currently recognizes 17 genera and estimates the number of species to be 600–700. "Spirit collections" of many of these species are available for anatomical work because of the research efforts of Raven and his collaborators. Another advantage in working with Onagraceae is that the taxa are diverse enough to be challenging, yet undoubtedly of common evolutionary origin. Among the characters that show the Onagraceae to be a natural family are the peculiar viscin threads on onagraceous pollen (Skvarla et al., 1977) and the distinctive 4-nucleate embryo sac (Seshavataram, 1970; Bhatnagar & Johri, 1972:91; Palser, 1975:641). Still another advantage is that the nearest extra-familial affinities of the Onagraceae are known to be among the myrtalean families Combretaceae, Crypteroniaceae, Lythraceae, Melastomataceae, Myrtaceae, Punicaceae, and Sonneratiaceae. Similarities in floral structure within this alliance were recognized by pre-Darwinian taxonomists and are now seen as indicators of shared ancestry, with strong con-

[1] I thank P. Raven and T. P. Ramamoorthy for criticizing the typescript. The National Science Foundation contributed indirectly, via a series of grants to Raven, by supporting the field work of several collectors. Photographs and anatomical preparations are the work of Smithsonian photographer V. Krantz and museum specialist S. Yankowski, respectively.

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firmatory evidence from such diverse sources as embryology (Subramanyam, 1951) and vegetative anatomy (Carlquist, 1975; van Vliet, 1975; van Vliet & Baas, 1975). Ideas on "ancestral versus derived" in the Onagraceae can be tested by looking into the related families for satisfactory distribution of the putative ancestral state.

Though the ultimate goal is to understand the evolution of the Onagraceae as a whole, this report concentrates on *Ludwigia* L., the only genus of the tribe Jussiaeeae (Raven, 1963). More than 70 species are known, all from wet habitats in temperate and tropical regions around the world (for illustrations, see Micheli, 1875; Rickett & Collaborators, 1967; Correll & Correll, 1972). Various authors have considered *Ludwigia*—or *Jussiaea*, now a synonym of *Ludwigia*—the primitive onagraceous genus (see Melchior, 1964; Takhtajan, 1966, 1973) because it seemed to provide the best link with adjoining families and because *Ludwigia* flowers were thought to retain ancestral traits, among them the 5(or more)-merous condition and the absence of a floral tube beyond the inferior ovary. It now seems that the absence of a floral tube is secondary in this case; moreover, it is now recognized that *Ludwigia* has a derived basic chromosome number and other specialized features. Undoubtedly, however, the genus represents an early evolutionary offshoot within the Onagraceae; a credible phylogenetic outline of the family must account for its peculiarities.

My wet material of *Ludwigia*, flowers from 30 collections belonging to 19 species, is listed in Table 1 along with nine collections from five more species (asterisked) that were available only as herbarium specimens. Altogether, these collections represent 10 of the 17 infrageneric sections recognized by Raven in 1963. Stained serial cross sections were prepared from all the collections and replicate series from most, also longitudinal series as needed, bringing to more than 100 the number of flowers (and developing fruits) sectioned and examined. Thanks to Raven and his collectors, I was able to compare the sectioned *Ludwigia* flowers with sectioned flowers from more than 70 additional species of Onagraceae, systematically selected from all parts of the family.

I begin with the androecium, though I have few new observations on *Ludwigia* stamens, because I want an unequivocal basis for discussing character associations, and I think all systematic botanists, despite differences in training and philosophical outlook, will accept the evidence for ancestral diplostemony in *Ludwigia*.

Androecium

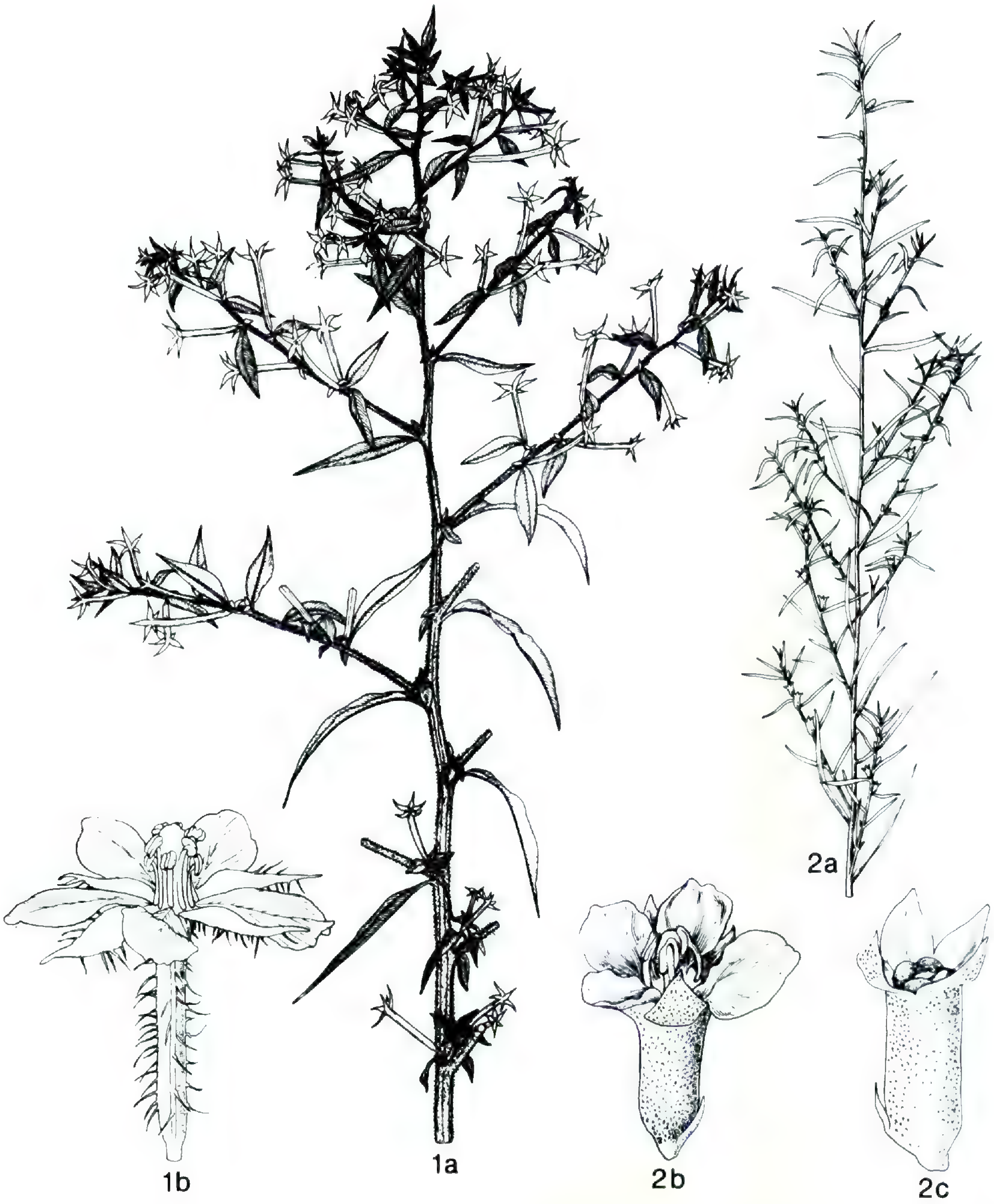
In general, *Ludwigia* species are constantly diplostemonous (the old genus *Jussiaea*, Fig. 1) or constantly haplostemonous (Fig. 2), but *L. perennis* can be intermediate (Raven, 1963), and at least one species, *L. inclinata*, includes some plants with two whorls of stamens, others with one whorl (Raven, personal communication). One may be confident that diplostemony is the ancestral condition because of its wide distribution in the Onagraceae, haplostemony occurring (outside *Ludwigia*) only in two genera with highly specialized flowers (*Circaea*, *Lopezia*) and in specialized members of two other genera (one species of *Camissonia*, sect. *Eucharidium* of *Clarkia*). In neighboring families, stamens are

TABLE 1. Herbarium vouchers for sectioned *Ludwigia* flowers.[a]

Taxa	Vouchers
Sect. *Oligospermum*	
L. peploides (H.B.K.) Raven	*Raven 14529* (LA), California. *Raven 26493* (MO), Arkansas.
L. uruguayensis (Camb.) Hara	*Raven s.n.* (DS), California [Naturalized, Stanford Univ.].
Sect. *Oocarpon*	
**L. torulosa* (Arnott) Hara	*Cowan 38886* (US), French Guiana. *de la Cruz 3813* (US), Guyana. *Howard & Howard 9911* (US), Dominican Republic.
Sect. *Nipponia*	
**L. epilobioides* Maxim.	*Chien 207* (US), China.
Sect. *Seminuda*	
L. leptocarpa (Nutt.) Hara	*Chevalier 21* (DUKE), Florida. *Raven 26491* (MO), Arkansas.
Sect. *Fissendocarpa*	
**L. hyssopifolia* (G. Don) Exell	*Asplund 14132* (US), Peru. *Purpus 6973* (US), Mexico.
Sect. *Myrtocarpus*	
L. decurrens Walt.	*Broome 855, 896* (both DUKE), North Carolina. *Raven 26469* (MO), Arkansas.
**L. densiflora* (Mich.) Hara	*Macedo 3940* (US), Brazil.
L. erecta (L.) Hara	*Raven 21573* (DS), Costa Rica.
L. foliobracteolata (Munz) Hara	*Raven 21981* (DS), Costa Rica.
L. latifolia (Benth.) Hara	*Raven 21575* (DS), Costa Rica.
L. peruviana (L.) Hara	*Steinberg s.n.* (FAU), Florida.
**L. tomentosa* (Camb.) Hara	*Dawson 15154* (RSA), Brazil. *Gardner 2571* (US), Brazil.
Sect. *Macrocarpon*	
L. neograndiflora (Munz) Hara	*Krapovickas & Cristóbal 12089* (DS), Paraguay.
L. octovalvis (Jacq.) Raven	*Raven 21574* (DS), Costa Rica.
Sect. *Ludwigia*	
L. alternifolia L.	*Broome 851, 860, 862* (all DUKE), North Carolina.
L. maritima Harper	*Chevalier 18* (DUKE), Florida. *Arguelles 1* (MO), Mississippi.
L. virgata Michx.	*Broome 863* (DUKE), North Carolina. *Willingham 597* (MO), Georgia.
Sect. *Microcarpium*	
L. alata Ell.	*Arguelles 3* (MO), Mississippi.
L. glandulosa Walt.	*Broome 865* (DUKE), North Carolina.
L. linearis Walt.	*Broome 856* (DUKE), North Carolina.
L. pilosa Walt.	*Broome 861, 902* (both DUKE), North Carolina.
Sect. *Dantia*	
L. arcuata Walt.	*Chevalier 11* (DUKE), North Carolina.
L. palustris (L.) Ell.	*Broome 859* (DUKE), North Carolina. *Willingham 598* (MO), Georgia. *Arguelles 2* (MO), Mississippi.

[a] Asterisks mark species for which herbarium flowers were sectioned; for other species, liquid-preserved flowers were used.

commonly twice or more than twice the number of sepals, the haplostemonous exceptions being the apetalous genus *Crypteronia*, the myrtaceous genus *Myrrhinium* (with specialized inflorescences and stamens; McVaugh, 1968: 407), and certain members of the families Lythraceae and Melastomataceae. The androecia of Lythraceae are almost bewildering in their meristic diversity; how-



FIGURES 1–2. *Ludwigia* illustrations.—1. *L. leptocarpa.* Top of plant (a). × 0.3. Flower (b). × 1.7.—2. *L. linearis.* Top of plant (a). × 0.3. Flower (b) and fruit (c). × 3.3. Partly redrawn by A. Tangerini from illustrations prepared by G. Reinert for R. K. Godfrey, who kindly lent the originals for copying.

ever, the fact that some of the haplostemonous taxa have stamens opposite the petals and others have stamens opposite the sepals is best explained by deriving both forms from precursors with at least two whorls of stamens. In the Melastomataceae, haplostemony is very much a minority trait, but a widely scattered one, occurring in seven New World genera (Wurdack, 1971: 360) and at least

five Old World genera: *Blastus*, *Dactylocladus*, *Dissochaeta*, *Omphalopus*, and *Sonerila*. I am assured by melastome specialist J. Wurdack that this taxonomic distribution indicates multiple evolutionary derivation of haplostemony within the family. Returning to the Onagraceae, we find in the genus *Ludwigia* itself that the woodier tropical species are mostly diplostemonous, whereas temperate species with such advanced features as poricidal capsules or apetaly are haplostemonous, still another indication that diplostemony is ancestral.

The stamens of *Ludwigia* species are much alike externally except for those of sect. *Ludwigia*. In this section, the filament joins the versatile anther in a deep dorsal groove, and the halves of the anther are parallel during development; consequently, the cross section is decidedly H-shaped, unlike that of a developing anther in other sections of the genus (cf. Figs. 3–4).

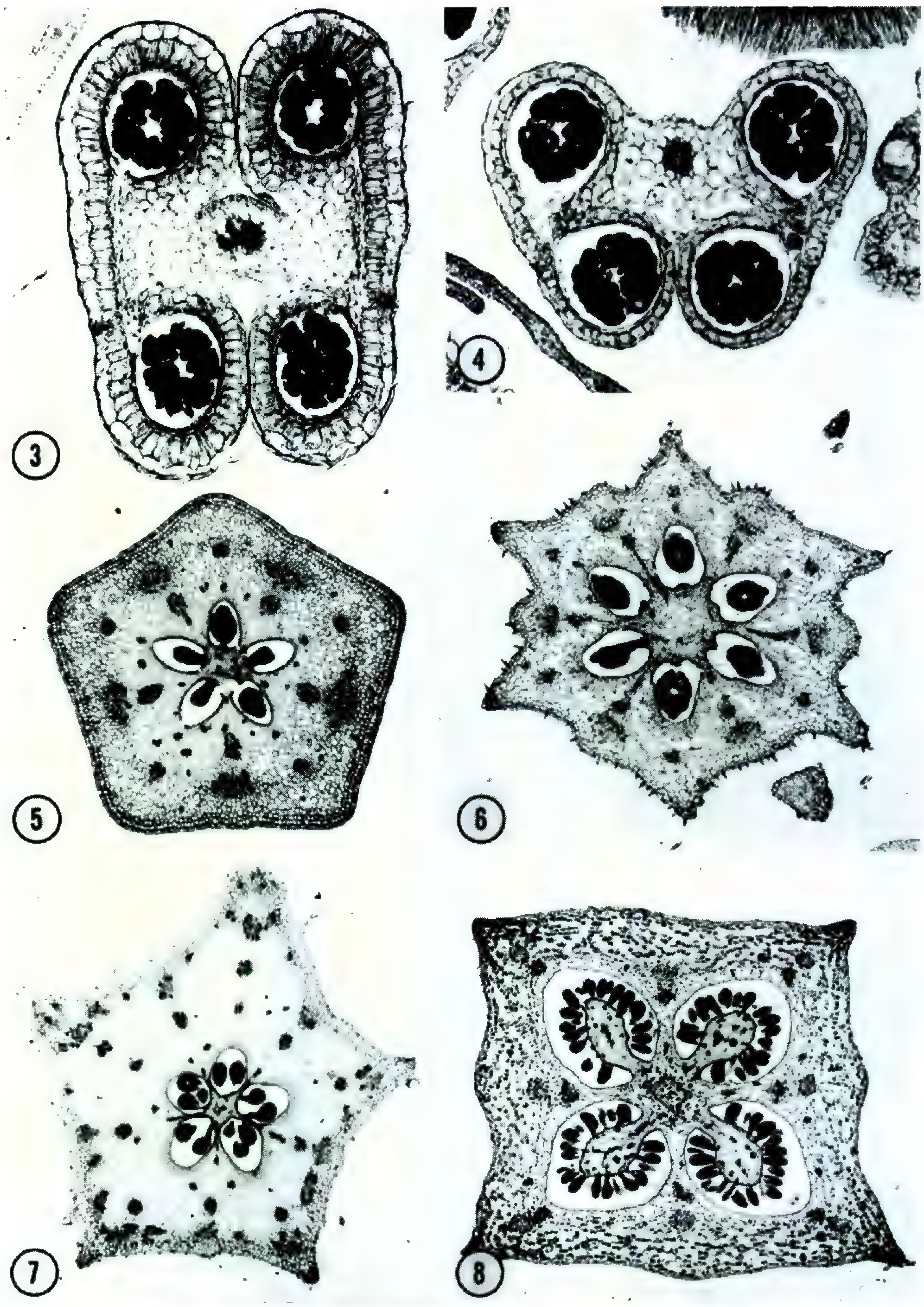
All the examined ludwigias have a conspicuous endothecium or "fibrous" layer. That is, the hypodermis of the anther is a layer of relatively large cells with narrow wall thickenings. As regards the development of the endothecium, *Ludwigia* anthers are like anthers of *Circaea*, *Hauya*, and certain fuchsias (e.g., *F. arborescens*); they are unlike anthers of *Clarkia*, *Gaura*, and *Gayophytum*, in which the endothecial cells are notably smaller than the epidermal cells. Future studies of onagraceous flowers should take careful note of the anther wall, for there are clear-cut endothecial differences not only among the genera but also within certain genera (*Epilobium*, *Fuchsia*). A prominent endothecium is probably ancestral (see Eames, 1961: 138 ff.); so these differences could turn out to be valuable evolutionary clues.

In my material of *Ludwigia latifolia* and of *L. linearis*, the developing pollen grains are in packets that are separated from other packets above and below by bands of parenchyma. This observation is of more than passing interest because interrupted sporogenous tissue was known heretofore in only five onagraceous genera—*Hauya* and four genera of the tribe Onagreae—and Raven (1969: 161) has argued, contra Munz (1965), that the shared character makes *Hauya* a member of the Onagreae. Discovery of pollen packets in another tribe, where they appear to have evolved twice, undermines Raven's argument and makes *Hauya*'s placement problematic.

PLACENTATION

In certain *Ludwigia* species, notably those of sect. *Oligospermum* and *Seminuda*, the ovules are inserted in 1-seriate rows, one vertical row to each locule (Figs. 5–6). In sect. *Ludwigia*, *Macrocarpon*, and *Myrtocarpus*, pluriseriate ovules are crowded on deeply intrusive placentas that are commonly spatulate in cross-section (Fig. 8). Sections *Dantia* and *Microcarpium* also have pluriseriate ovules, but the placentas are not spatulate in cross section (Fig. 9). In *L. epilobioides*, the ovules are 1-seriate in most locules; they can also be more or less 2-seriate (irregularly so), and both arrangements can occur in the same ovary. *Ludwigia hyssopifolia* is unusual in that the ovules are irregularly pluriseriate at the distal end of the placentas and 1-seriate below; I have observed the same situation in one collection of *L. leptocarpa*, sect. *Seminuda* (Fig. 7).

In all its variations, *Ludwigia* placentation has advanced beyond that of most



FIGURES 3–8. *Ludwigia* flowers in cross section.—3. *L. alternifolia*, *Broome 862*. H-shaped section of anther. × 80.—4. *L. decurrens*, *Broome 855*. Comparable section. × 100. In both figs., the abaxial side of the anther is up.—5. *L. peploides*, *Raven 14529*. Section passes through two of the five uppermost ovules and through the funicular attachments of the other three. × 28.—6. *L. leptocarpa*, *Raven 26491*. An ovary with all ovules 1-seriate. × 30. —7. *L. leptocarpa*, *Chevalier 21*. Here the upper part of the ovary contains pluriseriate ovules. × 20.—8. *L. foliobracteolata*, *Raven 21981*. Note deeply intrusive placentas. × 17.

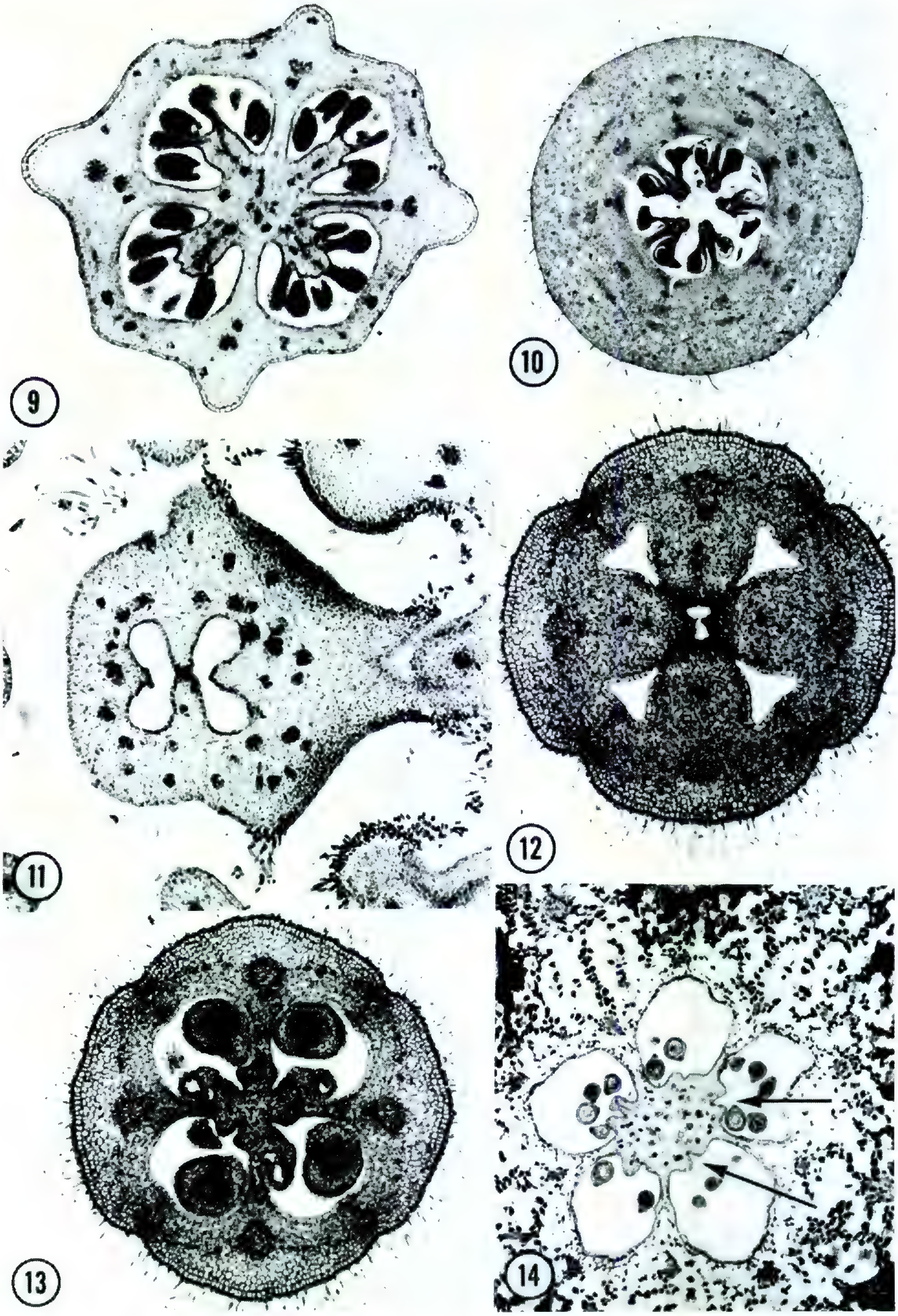
Onagraceae, for one rarely finds a vestige of the ancestral bipartite placental structure, and an actual separation of the ovarian septa (opening of the ventral sutures) can be found only by following them upward into the style (Fig. 11). This reasoning may seem uncritically "classical" to some readers; so I shall take pains to explain.

If we begin with the formalistic concept of carpel closure endorsed by Eames and others before him, then visualize the divisions of the onagraceous ovary as imbedded carpels and the placentas as fused carpel margins, we can say of *Ludwigia* that "the fusion is anatomically complete and the placenta is simple in form and structure" (Eames, 1961: 205). To be sure, evolutionary morphologists now find Eames's interpretation of syncarpy inadequate because it does not take into account a change in gynoecial ontogeny that has occurred within many groups, including the Myrtales—namely, a shift in the locus of septal development and ovule inception from discrete carpel primordia to a more recently evolved tubular meristem (the gynoecial cylinder of Sattler, 1973) beneath the carpel primordia. And associated with the origin of the Onagraceae there has been a further modification of the ontogenetic sequence so that the ovules now develop on septa growing upward and inward from a meristematic tube underlying the gynoecial cylinder as well as all the floral primordia (Sattler, 1973). It is not altogether wrong, however, to view the angles formed by the ovarian septa as fused carpel margins, at least in the upper part of the ovary where the septa are ingrowths that actually unite as the ovary develops. After all, the septa do not arise in random positions. They are initiated in line with the ends of the crescent-shaped carpel primordia above them, presumably under the morphogenetic influence of the carpel primordia.[3] Moreover, when the developing onagraceous flower first produces septa, then placentas, then ovules within its inferior ovary, it repeats a canalized sequence that began in distant ancestors with superior, apocarpous gynoecia. One cannot argue otherwise, I think, without opting for polyphylesis of angiosperms. As the gynoecium changed from apocarpus to syncarpous and from superior to inferior, the placentas continued to develop from the inner portions of the septa, and the septa continued to develop in vertical alignment with the margins of the increasingly ephemeral carpel primordia. (In *Ludwigia*, carpel primordia persist only as obscure stigmatic lobes.) From the evolutionary standpoint, therefore, the upper part of the ovary in many Onagraceae does contain carpel margins, even though they are no longer direct outgrowths from the carpel primordia, and the degree to which these margins

[3] In *Lythrum salicaria* (Lythraceae), where the two carpel primordia appear fleetingly, if at all, the location of the ovary's partition is not fixed. Within a single inflorescence, one may find some ovaries divided in the median plane, others in the tranversal plane (Sattler, 1973).

→

FIGURES 9–14. Onagraceous flowers in cross section.—9. *Ludwigia palustris*, *Willingham 598*. Placentas do not have the swollen appearance of those in Fig. 8. × 52.—10. *Hauya elegans*, *Breedlove 6432*. Ovary of a 5-merous flower showing discrete carpel margins. × 12.—11. *L. octovalvis*, *Raven 21574*. Base of style showing separation of septa; a stamen diverges at right. × 45.—12. *Epilobium fleischeri*, cultivated at the Royal Botanic Garden, Edinburgh,



as *C8092*. Uppermost level of ovary showing separation of septa. $\times$ 53.—13. Same flower, section taken about 600 μ below Fig. 12 showing median placental grooves. $\times$ 53.—14. *L. peruviana*, *Steinberg s. n.* Level of divergence of floral appendages showing distinct median grooves (arrows) in two of the placentas. $\times$ 20.

are fused can be an indication of evolutionary advancement. I have argued elsewhere that the union of carpel margins has reversed to some extent in certain Rosaceae (Eyde, 1975). For angiosperms as a whole, however, I accept the generalization that fused margins are derived and unfused margins ancestral.

To test the applicability of this generalization to the Onagraceae, we can compare gynoecia of the woody tropical genus *Hauya* with gynoecia of *Epilobium*, a predominantly herbaceous genus of temperate and cold regions. If we were to take serial cross sections of a *Hauya* flower and project them rapidly on a screen, proceeding from base to apex, we would see the septa separate within the ovule-bearing region (Fig. 10). If the sections were from a fully developed flower, the radii along which the septa part would be marked by pollen-transmitting tissue. If the projected sections were from a flower of *Fuchsia*, another woody tropical genus, septal separation would also be observed within the fertile part of the ovary. But a similar sequence through an *Epilobium* flower would differ in that the septa would not separate, if at all, until we had gone beyond the ovules into the very summit of the ovary (Fig. 12). The ontogenetic explanation for this difference is that the zone of septal upgrowth is relatively greater in *Epilobium* and the zone of septal ingrowth relatively less (Kaienburg, 1950: 400). Despite the fact that the zone of septal ingrowth is confined to the uppermost part of the ovary in the finished flower of *Epilobium*, each plane of septal fusion can be followed downward through much of the ovary because its position is marked by a median groove in the placenta (Fig. 13). Similar placental grooves occur in most onagrads, even those with only one ovule per locule, though they are not always as distinct as they are in *Epilobium*. The taxa I have found to be exceptional—that is, lacking a well-marked placental groove—are *Circaea*, two species of *Oenothera* (*O. campylocalyx*, *O. rosea*), and most species of *Ludwigia*.

In some species of *Ludwigia*, such as *L. hyssopifolia*, an observer passing through the gynoecium from base to apex might enter the style before seeing the separation of the septa, but in certain species of sect. *Myrtocarpus* and its derivative sect. *Ludwigia* there is an "elevated disc" below the style (see Micheli, 1875, for illustrations) in which the parting of the septa can be observed. Furthermore, it is only in species belonging to these two sections (*L. latifolia*, *L. peruviana*, *L. virgata*) that I have seen any trace of a placental groove, and then only in the upper part of the ovary (Fig. 14). If my reasoning with regard to ancestral and derived placental characters is correct, these observations place sect. *Myrtocarpus* near the ancestry of the genus, though its deeply intrusive placentas are advanced over those of most Onagraceae.

If we test the argument by considering the taxonomic distribution of bipartite placentas and partially unfused margins in related families, we find the distribution to be consistent with the view that these features are ancestral. In the Myrtaceae, a family closer than the Onagraceae to the ancestry of the Myrtales, taxa with partially unfused margins within the ovary are found among the capsular groups as well as the fleshy-fruited groups (Ludwig, 1952). In the Lythraceae, the small tree *Lagerstroemia indica* has separate septa in the summit of the ovary, whereas the slender herb *Lythrum salicaria*, a more advanced member

of the family, has neither separate septa nor grooved placentas (personal observations). Looking into the Sonneratiaceae, Cronquist's (1968) choice as the most nearly ancestral myrtalean family, we find that the septa are separate in the upper fifth of the *Sonneratia* ovary (Mahabalé & Deshpande, 1957). To judge from published illustrations, the ovaries of *Duabanga*, the only other genus of the Sonneratiaceae, are structurally similar (Jayaweera, 1967: figs. 1J, 3F). In the highly specialized flowers of Melastomataceae, however, the septa part in the style (van Heel, 1958) or not at all (Eyde & Teeri, 1967; Subramanyam & Narayana, 1969).

Derived Status of 4-mery

The evolutionary morphologist of a few decades ago might have claimed derived status for 4-mery without risking contradiction, at least from American colleagues, on the principle that the "polymerous flower structure precedes, and the oligomerous structure follows from it" (Bessey, 1915). Many exceptions to this principle are known (Stebbins, 1967), however, and Huether's experiments on *Linanthus* (summarized by Stebbins, 1974) have shown how readily the number of floral parts can be increased as well as decreased under selective stress.

In *Ludwigia*, moreover, higher numbers of floral parts can occur in association with certain advanced features. For instance, in sect. *Oocarpon*, with 5-merous flowers, and in sect. *Oligospermum*, where 5-mery is the rule and 6-mery occasional, the higher numbers are linked with 1-seriate ovules and a specialized endocarp. In sect. *Seminuda*, with 4–7-merous flowers, the ovules are also 1-seriate, though the fruits are specialized in a different way. Another example is *L. epilobioides* (sect. *Nipponia*), a self-pollinating herb of temperate Asia in which 4–6-mery is associated with haplostemony. Raven (1963) reports that 5-merous flowers can be found, albeit rarely, in *L. perennis* (sect. *Caryophylloidea*); this species too is commonly haplostemonous. In *Myrtocarpus*, the "phylogenetically central" section of *Ludwigia* (Raven, 1963), *L. densiflora* has 4–6-merous flowers in a spicate (derived) inflorescence, and *L. peruviana*, in which 5-mery is encountered fairly often, is an aggressive polyploid colonizer. (On the other hand, T. P. Ramamoorthy informs me that 5-mery is the usual condition in the Brazilian shrub *L. tomentosa* and that he has seen 5-merous flowers in a number of other species belonging to sect. *Myrtocarpus*.)

Excepting these sections—and sect. *Prieuria* with mostly 3-merous flowers (Raven, 1963)—4-mery is quite constant in the genus *Ludwigia*. I have seen no 4+-merous flowers in sect. *Dantia*, *Macrocarpon*, or *Microcarpium*; and in sect. *Ludwigia*, I have seen only two 5-merous flowers of *L. virgata* and no other exceptions. Throughout the remainder of the family, 4-mery occurs with similar constancy (though the flowers of a few taxa regularly have fewer than four parts). A minority of *Hauya* flowers are 5-merous and five stigmatic rays can occur in *Oenothera* (Cleland, 1972: 6), also in at least one species of *Epilobium* (*E. dodonaei*, personal observation), but I do not know that 5-mery or partial 5-mery has ever been observed in *Fuchsia*, a genus seemingly as close as any to the ancestry of the Onagraceae.

In the Onagraceae, therefore, ancestral status might be claimed for 4-mery

on the grounds that 4+-mery is almost exclusively confined to *Ludwigia*, where it often accompanies derived characters. This reasoning runs into difficulty, however, when the reconstruction of onagraceous ancestry is extended beyond the family limits, for the ancestral Myrtales surely had more than four floral parts per whorl. To claim 4-merous ancestry for the Onagraceae, one would have to begin with myrtalean ancestors in which floral parts were indefinite in number; then postulate a derived group, ancestral to all Onagraceae, with floral parts stabilized in whorls of four; then further postulate a return to 4+-mery in each of several lines within *Ludwigia*. An evolutionary scheme incorporating these steps would be less economical than one in which 4-mery is treated as a derived character.

Stebbins (1967) has pointed out that the number of floral parts in a whorl is partly dependent on the number of cells in the floral apex at the time the whorl is initiated; so it is not surprising that higher numbers are often found in larger flowers. The relationship between meristem size and numbers of parts may explain Müller's (1870) observation that individual plants of Brazilian ludwigias (species unspecified) tend to produce 5-merous flowers first, 4-merous flowers later (see also Huether, 1968: 128), but there is no consistent relationship between floral size and merism in *Ludwigia*. Some large-flowered species are constantly 4-merous, whereas *L. torulosa*, with very small flowers, is constantly 5-merous.

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Preliminary Announcement

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Sydney, Australia. 21–28th August, 1981

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PERSPECTIVES IN TROPICAL BOTANY: INTRODUCTION

P. B. TOMLINSON[1] AND PETER H. RAVEN[2]

The following papers were presented at the Symposium entitled "Perspectives in Tropical Botany," held 22 August 1977 during the 28th Annual Meeting of the American Institute of Biological Sciences, Michigan State University, East Lansing. It was cosponsored by the Botanical Society of America, Ecological Society of America, American Society of Naturalists, and American Society of Plant Taxonomists.

Intensified studies of the plants, vegetation, and ecosystems of the tropics is not some esoteric or arcane aspect of pure science but essentially an area of applied biology which is much neglected. A number of familiar factors contribute to a feeling of urgency among tropical plant biologists which lead to this small symposium:

(a). The greatest concentration of floristic and functional diversity occurs in the tropics.

(b). There is a relative dearth of active research scientists in the field of tropical botany.

(c). Tropical ecosystems are being destroyed at a rapid rate without adequate compensation in terms of conservation of representative vegetation types and of genetic resources.

The total effect is one of an overall deficiency in our understanding of biological processes in plants, which is unfortunate since it occurs within countries which have predominantly agriculturally based economies with plants as a major natural resource. This message is stated to the point of tedium, but it needs constant attention by professional biologists.

This symposium emphasized that this imbalance presents a problem of universal concern. Tropical botany is not a discipline set apart from the rest of

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plant science—it is an essential aspect of the whole subject, and for this reason any deficiency in our understanding of tropical vegetation is detrimental to our total understanding of the biology of plants. Any comparative study of plant form or structure is based on incomplete premises if it does not take into consideration the total range of natural variability in plants, i.e., including the enormous diversity of plant life in the tropics. Any physiological mechanism or ecological response has been analyzed insufficiently if it does not consider how these mechanisms or responses are mediated in tropical climates and especially in the nonseasonal climates of the lowland tropics. Any evolutionary idea has been incompletely scrutinized if it has not been tested against tropical examples. Any generalizations of plant population biology must apply to the frequently distinctive composition of tropical forests.

And yet this cosmopolitan consideration is frequently lacking because of the enormous geographical paradox that besets biology—namely, it is temperate based, with its practitioners trained and deployed within relatively depauperate temperate ecosystems. The paradox is heightened by the fact that the greatest repository of known information about tropical plants resides in the herbaria and libraries of temperate countries.

The object of the Symposium was to call upon a group of contributors, chosen because of their wide research experience in the tropics, and ask them to comment upon the present status of an aspect of tropical plant science wherein they are acknowledged experts. The further suggestion was made that they assess future needs in tropical research, although this was not a prime requirement.

Tropical biology has developed enormously in the United States since World War II partly by the efforts of a number of institutions which have emphasized the discipline and particularly by the concerted action of a group of Universities that led to the formation of the Organization for Tropical Studies which has provided a mechanism whereby a generation of biology students have been introduced to the tropics. An overview of an important aspect of tropical science is therefore appropriate at this stage, and we hope that the limited opportunity for presentation which this Symposium permits will generate further interest and action in the field of tropical botany. Whether we look back over what has been achieved or forward to what has still to be done, the opportunity for a brief appraisal is a welcome one.

The twentieth century draws rapidly to its end—a century in which scientific advance has wrought endless miracles, culminating in the technological expertise which allows us to explore the universe directly. How unbalanced might our perception become before we discover that too little has been done too late to allow us to understand our more immediate environment, which after all provides us with food, energy, shelter, and an abundance of natural, renewable resources—the environment provided by the plant kingdom.

FLORISTIC INVENTORY OF THE TROPICS: WHERE DO WE STAND?[1]

Ghillean T. Prance[2]

In a review of the vast topic of the inventory situation in the entire tropics I can only skim over the surface. I have aimed to pinpoint a few of the significant contributions (many other important ones are omitted) and to draw attention to some of the areas in need of further work. These include both geographical areas that are poorly collected and disciplines which are still neglected in our basic survey of the fascinating vegetation of the tropics. There is still a great deal to be done and time is running out as the natural vegetation is being destroyed. Brazier et al. (1976) said: "More efficient use of the natural tropical forest could be achieved if sufficient information on the extent, composition and structure of the resources were available."

The data which we collect from botanical inventory are not only useful for the study of floristics and evolution, but are also of vital importance for both conservation and utilization of the tropical vegetation.

Of What are We Making an Inventory?

Table 1 gives a summary of the estimated number of species in the different major plant groups, compiled from the best available sources. The tropical flora consists of some 155,000 species of flowering plants, 11,000 ferns and fern allies, 16,000 bryophytes, and at least 90,000 fungi. The tropical flora is by far the richest in species diversity, yet it is also the most poorly collected. This diversity is being reduced before we have made an adequate basic inventory let alone conducted modern biosystematic and population biology studies in the area. Even to understand the origin and dynamics of our temperate flora, it is essential to have adequate knowledge of the tropical flora from which the temperate flora was derived.

Tropical Africa has the smallest number of angiosperm species, 30,000, including various islands and the 10,000 species of Madagascar (Koechlin, 1972). Tropical Asia, Australia and the Pacific have at least 35,000 species, and tropical America has about 90,000 species or 37.5% of the worldwide total. Unfortunately, the state of knowledge of these floras is also inversely proportional to the species diversity, with the American tropics much more poorly known than the African and Asian tropics.

In any discussion of inventory of the tropical flora it is important to consider habitat diversity and species diversity. We tend to ignore the habitat diversity of the tropics which contributes to its species richness, and to think of it as one

[1] I am grateful to the many people who have helped to provide information about the areas of their specialty especially to Mr. F. N. Hepper, Drs. F. R. Fosberg, M. Jacobs, Alain Liogier, W. Meijer and A. Gentry. I thank Mr. W. C. Steward for much bibliographic assistance, Mrs. F. Maroncelli who typed the manuscript, and Drs. Howard Irwin and Scott Mori for reading the manuscript critically.

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TABLE 1. Estimated species numbers of major plant groups in the world and in the tropics. Data compiled from many sources such as Ainsworth (1961: 405–407), Jacobs (1974, 1977), and Raven (1976a).

Taxa	Worldwide	Tropical	Tropical Africa	Tropical Asia	Tropical America
Flowering Plants	240,000	155,000	30,000	35,000	90,000
Fungi	120,000[a]	90,000	20,000	20,000	50,000
Ferns	12,000	11,000	1,000	6,000	5,000
Mosses	12,000	9,000	—	—	—
Hepatics	11,000	7,000	—	—	—
Algae	17,000	—	—	—	—
Lichens	16,500	—	—	—	2,500

[a] Other estimates for fungi are as high as 250,000 species, e.g., Martin (1951), Jones (1951), and Rogerson (pers. comm.).

large uniform rain forest. In fact, the tropics contain many arid regions with deserts or scrubland, such as the caatingas of northeastern Brazil, a large temperate element in the flora of high mountains, and a unique alpine flora such as that of the páramos in South America and the Afro-alpine region described by Hedberg (1964), besides many different types of forest and savanna. The habitat types of Malesia were summed up by Jacobs (1974), those of South America by Hueck (1966), and those of Africa by White (in press) in a book to accompany the second edition of the UNESCO vegetation map of Africa. There is not time here to summarize the fascinating diversity of habitat in the tropics, but it is important to collect from and to plan conservation of this habitat diversity. Until now collecting has given rather uneven coverage to the different habitats. The location of different habitats has been overlooked frequently in biogeographic analyses of the neotropical vegetation, although the inventory of habitat distribution is vital to biogeographic studies.

WHAT IS LEFT TO INVENTORY?

The tragedy of the biological inventory of the tropics is that destruction of the vegetation is proceeding more rapidly than the inventory. The tropical flora occurs mostly within the territory of developing countries where technological advance is urgent. Such advance traditionally includes the destruction of large areas of natural vegetation for replacement by farms, timber concessions, developing towns, etc. In addition there is population pressure in many tropical countries where the annual net population increase is often over 3% (see, for example, The Environmental Fund, 1976).

Many authors have drawn attention to the destruction of the natural vegetation in the tropics, for example, Gómez-Pompa et al. (1972), Richards (1973), Janzen (1974), Holdridge (1976), Myers (1976), Raven (1976b), Gentry (1978b), and many of the authors in Prance & Elias (1977). It is not the purpose of this paper to review in detail the destruction of the tropical vegetation, but as the tropical areas are vital for the understanding of the biology and evolution of all plants, it is important to draw attention to the urgent need to accelerate all biological inventory and conservation work in the tropics. According to recent

estimates 49.2 acres of tropical rain forest are being removed each minute or a total of 11,000,000 hectares a year (Lucas, 1977; Sommer, 1976). Inventory work daily becomes a more important task to perform, as destruction of natural habitats encroaches. Since there is not a separate treatment of conservation in this symposium, I feel that it must logically be stressed as part of the inventory. It is not possible or profitable to list examples of tropical destruction from each area discussed below, but I draw attention to this race between inventory and destruction in the tropics and hope that we can also focus our efforts more towards conservation. None of the other subjects treated at this symposium can be completed without the conservation of large areas, and without a comprehensive basic inventory.

The Regional Status of Inventory

AFRICA

Progress on the status of systematic work in tropical Africa is readily accessible through the publications and symposia of the "Association pour l'étude taxonomique de la flore de l'Afrique Tropicale" (AETFAT). This organization publishes an annual index which includes a bibliography and lists of new taxa and nomenclatural changes for all tropical African plants. Progress reports on collections, the regional floras, mapping, etc., are given in the proceedings of their symposia which take place every fourth year (see, for example, Hedberg & Hedberg, 1968; Kubitzki, 1971). AETFAT plays a similar role for Africa as *Flora Malesiana* does for Asia in making available much information and bibliographic data invaluable for research in the area. A review of the current status of collecting in tropical Africa was given by Hepper (in press).

Léonard (1975) prepared, for AETFAT, a map of the extent of floristic exploration in Africa south of the Sahara up to 1963. This map divided the region into 3 categories: poorly known, moderately known and well-known areas. Hepper (in press) gave up-to-date information of changes to this map and a revised edition will be presented at the 1978 AETFAT Congress.

The *Flora of Tropical Africa* (Oliver, 1868–1937) is the only attempt at a general flora of the region. This has been largely replaced by the modern regional floras, especially the *Flora of West Tropical Africa* (recently revised), *Flora of Tropical East Africa*, and *Flora Zambesiaca*. Current African floras are summarized in Table 2.

Statistics for the description of new taxa in Africa from 1953–1965 were summarized by Léonard (1968) and showed a gradual decline from 1,177 new names (577 new species) in 1953 to 723 new names (287 new species) in 1965. The rate of description of new species continued at approximately the same rate in 1971–1975 and is shown in Fig. 1. The fact that 270 new species were described in 1975 shows that the basic species inventory of the African flora has not yet ended. Figure 1 also shows the amount of synonymy proposed in the years 1971–1975 (data from the AETFAT indices). It shows that there is apparently a gradual drop in the net gain in species because of increasing synonymy, 218 net gain in 1971 as compared with 119 in 1975. Nevertheless, the total

TABLE 2. Principal regional floras of tropical Africa.

Publication		Editor or Author
Flora of West Tropical Africa	ed. 1	Hutchinson & Dalziel (1927–1936)
	ed. 2 revised by	Keay et al. (1954–1972)
Flora of Tropical East Africa		Turrill & Milne-Redhead (1952–)
Flora Zambesiaca		Exell & Wild (1960–)
Flora of Egypt		Laurent-Täckholm (1941–)
Flore du Sénégal		Berhaut (1954, 1967)
Flore du Gabon		Aubréville (1961–)
Flore du Cameroun		Aubréville (1963–)
Flore du Congo, du Rwanda et du Burundi		Robyns (1948–)
Syllabus de la Flore du Rwanda		Troupin (1971)
Conspectus Florae Angolensis		Carrisso (1937–)
Prodromus einer Flora von Südwestafrika		Merxmüller (1966–)
Flora of Southern Africa		Codd et al. (1963–)
Flore de Madagascar et des Comores		Humbert (1936–)

number of new descriptions in Africa south of the Sahara for the 21 year period, 1953–1973, are impressive: 391 new genera, 7,478 new species, and 2,538 infra-specific taxa. That is a new genus every 3 weeks and a new species for every day of the 21 years (data from Hepper, in press). A flora in this active state of description that is still adding 1,000 new species over a five-year period is obviously also in need of further collecting. Many of the reports on the progress of various African floras given in Kubitzki (1971) include emphasis on the need for further collecting, for example, Boulos (1971) for Libya, Aké Assi (1971) for the Ivory Coast, Le Thomas (1971) for Gabon, etc.

Distribution maps of African taxa such as those published by Bamps (1969) in the very useful series "Distributiones Plantarum Africanarum" (see Fig. 2), show that the African flora is really well explored in comparison with the Neotropics. For this reason more analytical phytogeographic papers have come from taxonomists working on the African flora. The better known plant distributions have enabled much better phytogeographic analysis of the flora, see, for example, White (1962, 1965, 1971), the introductory chapters in Chapman & White (1970).

Hepper (in press) summarized the collecting situation in Africa as still having large gaps. He said that general collections are now required only from lesser known regions, and he stressed the need for specialist collections and for resident botanists to carry out long-term investigations. He pointed out some particular gaps in collecting such as the tendency to collect mountain tops and ignore the forested slopes. For further information about Africa the reader is referred to Hepper's paper.

The native African flora has been disappearing rapidly under human popu-

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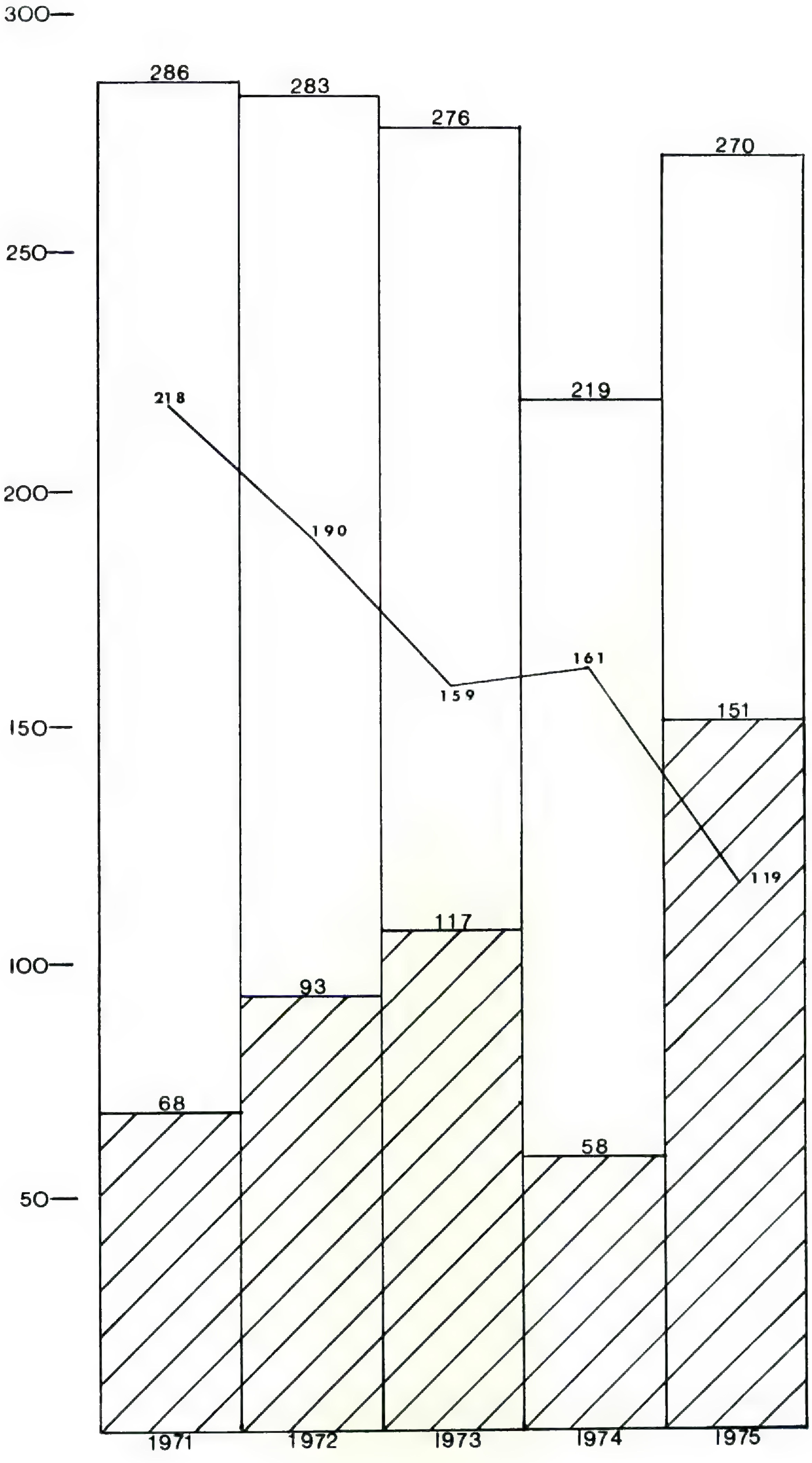
FIGURE 1. The description of new species in tropical Africa: data from the AETFAT Index, 1971–1975. The open area represents the total number of new species described, the cross hatched area superimposes the number of species names reduced to synonymy. The graph in the center represents the net gain in species each year.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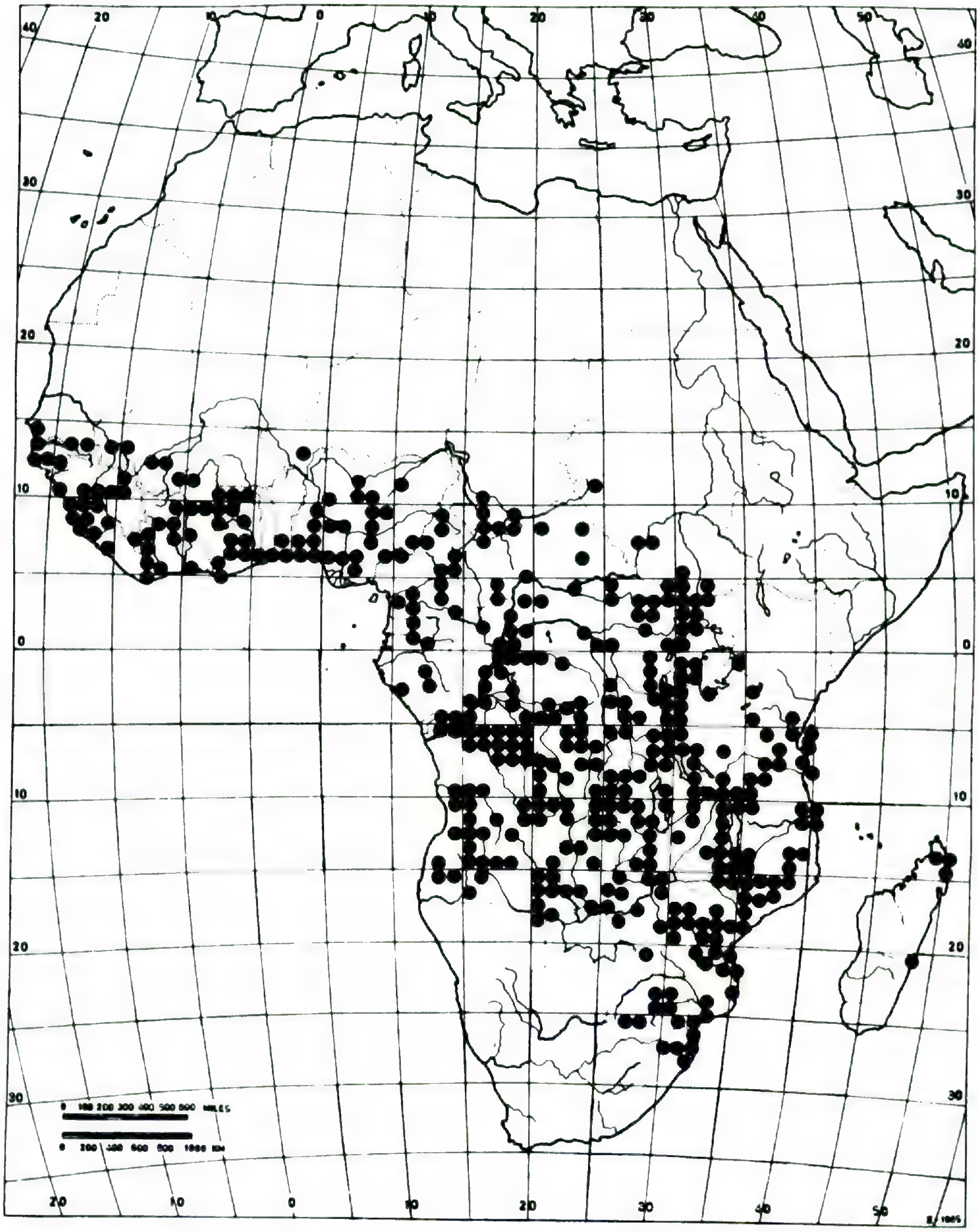

Chrysobalanaceae **327. - *Parinari* Aubl. (1775)** **F. White**

Synthesis tabularum 328-334

FIGURE 2. Distribution of the genus *Parinari* Aubl. (Chrysobalanaceae) in Africa: From White (1976) Distributiones Plantarum Africanum 10: 281–334. The dots represent presence in a degree square.

lation pressure for longer than that of Malesia or the neotropics. Shantz (1948) discussed the shrinkage of the tropical forests of Africa and Shantz & Turner's (1958) photographic account of the destruction of the vegetation of Africa is a frightening report for any biologist. Hepper (in press) also stressed the urgency for collecting the poorly known areas because of the rate at which the natural vegetation is disappearing.

In Madagascar, where the largest contributions have been made by H. Perrier de la Bathie and H. Humbert, the original species-rich forests have been almost totally disturbed (Gentry, pers. comm.), and the race to collect this exciting flora before it is obliterated is lost. Koechlin (1972) summarized the situation in Madagascar: "Many problems still have to be solved in the field: although the exploration of the flora is well advanced, much remains to be done in the areas of plant biology and phytosociology."

TROPICAL ASIA

The Asian tropics are probably not as well collected as Africa, but are much better known than the neotropics. Much information about tropical Asian botany has been compiled and published in *Flora Malesiana* and its extremely useful *Bulletin*, largely through the initial efforts of Professor C. G. J. van Steenis. The *Flora Malesiana* project covers Indonesia, Malaysia, Brunei, the Philippines, Singapore, eastern New Guinea, and the Solomon Islands. An excellent summary of the botanical status of the region has been given by Jacobs (1974). The situation has changed little since that report. The history of collecting in Malesia is given by Mrs. van Steenis-Kruseman (1950) in a "Cyclopaedia of Collectors" published in volume 1 of *Flora Malesiana* and updated from time to time in the *Flora Malesiana* and in the *Bulletin*, for example, van Steenis-Kruseman (1958, 1974, 1977). It is not, therefore, necessary to repeat the data given in these sources but rather to indicate some of the gaps in collecting as given below.

Dr. Jacobs (pers. comm.) lists the following places in Malesia as undercollected and in need of further basic inventory: The Andaman Islands, Southern Sumatra, Central Borneo, Celebes, Kabaena, Ceram (expedition planned), West New Guinea (especially Meerilakte and the Star Mountains in West Irian), the Kikari area in the south of Papua, the Philippines (especially the Sierra Madre on the east coast of Luzon), and the Cape York peninsula of Australia which has in recent times yielded several genera that were known only from Malesia. The northwest Australian coast is still poorly known. Perhaps Celebes is the least collected area and is now less known than New Guinea, especially the eastern and southeastern area of the island. Celebes also illustrates the race against development, since the International Nickel Company in cooperation with Bechtel has a billion dollar nickel mining concern in Celebes. Table 3 from *Flora Malesiana* reproduces their synthesis of the collecting situation in the larger units of Malesia. It points to the need for further collections from Sumatra and Celebes.

Jacobs (1977) has summarized the progress in the publication of *Flora Malesiana*. By the end of 1976, 116 families, 453 genera, and 3,288 species of angiosperms had been monographed out of an estimated total of 25,000 species. The fact that only 13.15% of the flora has thus far been published, together with the

TABLE 3. Collecting density (specimens/km^2) of Malesia (from *Flora Malesiana*, Ser. 1, 8(1): 3. 1974.).

	Surface (km^2)	Collected to 1950	Collected to 1972	Density Index 1950	Density Index 1972
1. Sumatra	479,513	87,900	99,000	18	21
2. Malay Peninsula	132,604	191,055	232,000	145	175
3. Java	132,474	247,522	260,500	187	197
4. Lesser Sunda Is.	98,625	24,545	36,000	25	36
5. Borneo	739,175	91,550	194,200	12	26
6. Philippine Is.	290,235	180,090	200,000	62	69
7. Celebes	182,870	32,530	34,000	18	19
8. Moluccas	63,575	27,525	30,400	43	48
9. New Guinea	894,855	106,775	233,000	12	26
Totals	3,013,926	989,492	1,319,100	$\bar{x} = 33$	$\bar{x} = 44$

figures for *Flora Neotropica* given below, shows the magnitude of the task in tropical areas and the shortage of botanists to work up the results of inventory. The slow production of monographs is a serious problem and lags behind the progress of development. However, a basic collecting inventory is more important before forests are destroyed. For Pteridophytes, *Flora Malesiana* has published 5 families, 14 genera, and 350 species or 14% of the estimated 2,500 species.

A comparison of the three major continental areas of the tropics in terms of statistics of species descriptions is not as straightforward as it may seem since the different status of knowledge in each flora has tended to result in a rather different species concept in each area. Although the tendency is toward much new synonymy in all three areas, the Malesian botanists seem to have a more conservative attitude to the species concept. For example, Leenhouts (1967) reduced all 255 species of *Allophylus* (Sapindaceae) to the single species *A. cobbe* (L.) Raeusch. Whitmore (1976) cites other examples. The concept of the reticulately polymorphic ochlospecies came from work on the African flora (White, 1962). The species concept in Africa lies somewhere between that of Malesia and the narrower concept that has predominated in the neotropics until recently. It is not the purpose of this paper to evaluate the merits of these different concepts, but an acknowledgement of their existence is necessary for a comparison of data between the different areas. Whitmore (1976) also pointed out the different kinds of species that exist in the tropics, accepting three kinds; the discrete, isolated and morphologically invariable species, the species with distinct infraspecific taxa, and the reticulately variable ochlospecies.

There are numerous local floristic works within the *Flora Malesiana* region, the best known of which is Backer & Bakhuizen van den Brink's (1963–1968) *Flora of Java*.

In the Asian tropics outside Malesia the situation is similar with a reasonable basic inventory but still some neglected areas.

India and Burma have had much less collecting since World War II, but a botanical survey of India is making good progress. In India there is a general reluctance to collect trees in primary vegetation and little specialist collecting

TABLE 4. Collecting status of some Pacific Islands: (1) only casual collecting; (2) poorly collected (not professionally collected); (3) moderately well collected; (4) rather well collected but some gaps; (5) quite well collected. More than one number means different islands in groups collected to different degrees. (Data from F. R. Fosberg, pers. comm.)

Island	Collecting Status		
Revillagigedo	3	Cook Islands	2, 3, 4
Cocos	2	Northern Cook Islands	3, 4
Galápagos	4	Wake Island	5
Easter Island	4	Marshall Islands, Northern	4, 5
Hawaiian Islands	4	Marshall Islands, Southern	3, 4
Phoenix Islands	5	Gilbert Islands	2, 3, 4
Other Central Pacific atolls	4	Naura and Banaba	1
Marquesas	3	Ellice Islands	2, 3
Society Islands (high)	2, 3	Niue Island	4
Society atolls	2, 3, 5	Rotuma Island	4
Tuamoto Islands	2, 3, 4	Wallis and Horne Islands	2
Makatea	2	Tokelau Island	3
Austral Islands	3, 4	Samoa Islands	4
Rapa	3	Tonga Islands	2, 3, 4

has been done. Some local floras are replacing Hooker's (1872–1897) *Flora of India*, as for example the recent *Flora of the Hassan District* by Saldanha & Nicolson (1976). Burma has had the smallest portion of its flora collected.

Thailand has had intensified general collecting since 1960 with a wide coverage of habitats and areas but little specialist collection. Collection has been stimulated by the joint Thai-Danish project on the *Flora of Thailand* under the leadership of Kai Larsen and Tem Smitinand and their collaborators.

Sri Lanka has been extremely well collected and worked up under the *Flora of Ceylon* project directed by F. Raymond Fosberg. This project has included much specialist collecting and the results of this are obvious in the resultant monographs.

Indo-China has had little collection since World War II except for a few vegetational studies in Laos and South Viet Nam. The political upheaval in that region has not been conducive to botanical inventory. The use of chemical defoliants in the war has truly devastated large areas of the forests of Indo-China.

The *Flora Malesiana Bulletin* serves a very fine role of reporting on progress in tropical Asian botany, even in countries outside the range of the *Flora* itself, and is commendable for the amount of useful information generated. The annual columns on progress in Malesian botany, expeditions and exploration, and on recent publications serve to keep us up to date on the state of Asian botany. There is a need for such a bulletin attached to *Flora Neotropica*.

For the tropical Pacific islands Dr. F. R. Fosberg has provided me with the data presented in Table 4. It shows that there are islands which remain poorly collected. Exact statistics on collecting are not available, but there is obviously much still to be done in this area that is so fascinating from the point of view of island biogeography. Dr. A. C. Smith has worked extensively in Fiji so that the archipelago can now be considered well collected, and he is following up with a flora of the islands.

THE NEOTROPICS

The New World tropics are certainly much less known than Africa or Asia and are still in the process of the first basic inventory. New species are still being collected in large numbers from many places, as, for example, the large number of new species from recent collections in the uplands of Panama, from coastal Ecuador, from the forests of the state of Bahia, Brazil, and from many other localities.

The collecting density throughout the neotropics is much less than for Malesia, but added to this, the greater number of species in the neotropical flora and the unevenness of collection throughout the area mean that the basic comprehensive species inventory is still most inadequate and by no means nearing its completion.

Unfortunately there is no equivalent of the *Flora Malesiana Bulletin* or the AETFAT publications in the neotropics. Thus, calculations of botanical activity are harder to make and are less accurate. We hope, however, that the Organization for Flora Neotropica will gradually begin to fill in this information gap as it begins to diversify its interest from only producing taxonomc monographs.

A comparison of many aspects of the ecosystems of Africa and South America is given in Meggers et al. (1973), but it does not cover the subject of inventory in any detail.

The last comprehensive review of the state of neotropical botany was that of Verdhoorn (1945). Much collecting has taken place since 1945 and some aspects, particularly from the conservation point of view, were surveyed in Prance & Elias (1977). In Prance (in press) I give a country-by-country review of the status of botanical exploration in South America, and Gentry (1978a) reviewed the floristic needs of Central America and the Pacific coastal region of northern South America. There is no space to give such a detailed review here, but a few examples will serve to show the situation in the neotropics.

Figure 2 is a distribution map of the pantropical genus *Parinari* in Africa from White (1976). The dots on the map represent presence in a degree square. Figure 3 is a similar distribution map of the same genus in the neotropics. The genus is common and widespread on both continents. It can be seen how much more densely the map of Africa is covered. Judging by the frequency of the individuals I have encountered in fieldwork in the neotropics and by the number of habitats occupied by the different species, I would predict that to be accurate the neotropical map should be almost as densely covered with dots for each degree square as is Africa, and that the distribution difference is actually the result of inadequate collections in South America.

Gentry (1978b) reported on an expedition to Cerro Tacarcuna, a previously unexplored mountain on the Panama-Colombia border. At least 20% of the 239 species collected above 1,400 m have turned out to be new. A similar figure is

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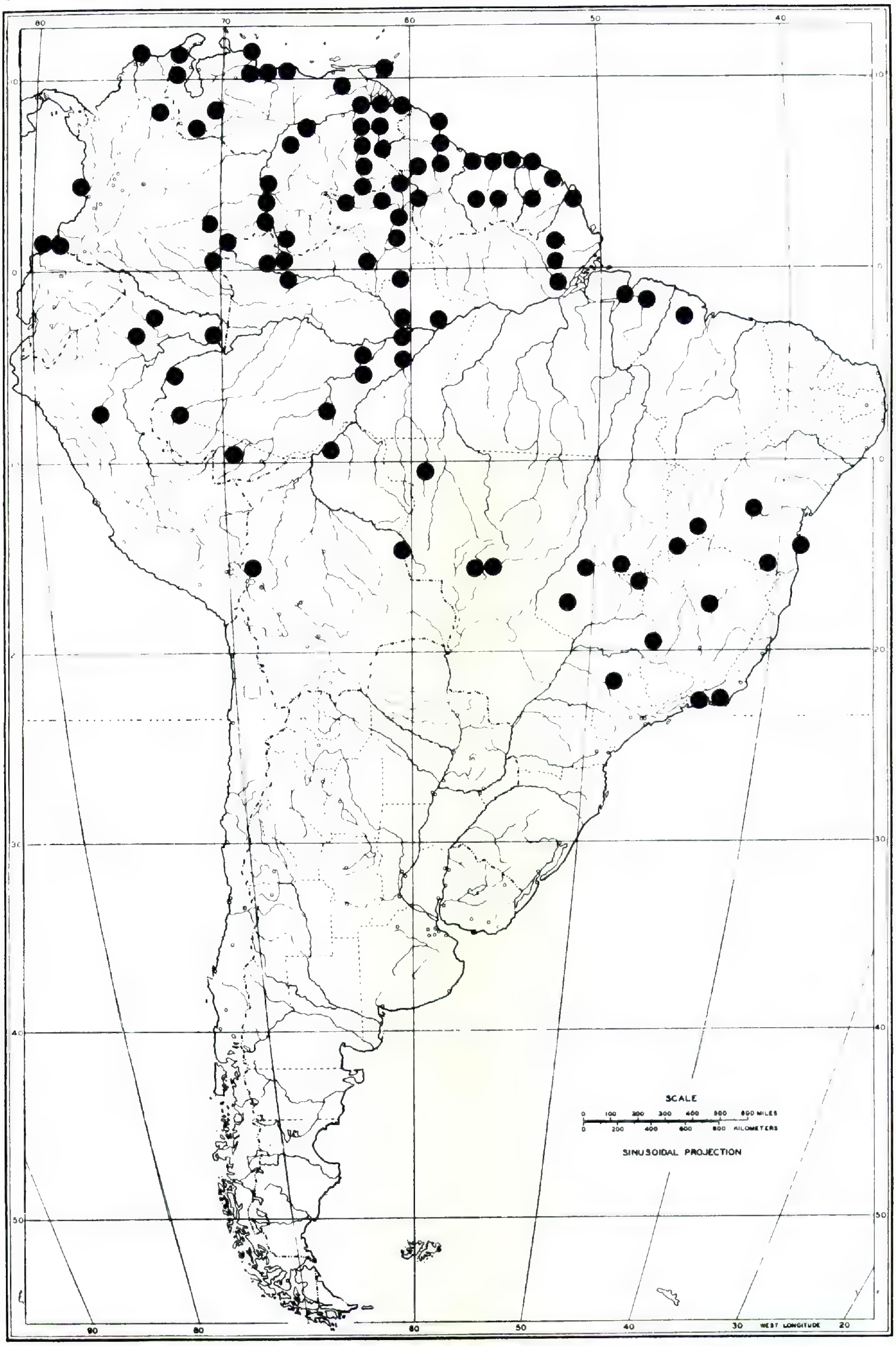
FIGURE 3. Distribution of the genus *Parinari* Aubl. (Chrysobalanaceae) in South America. The dots represent presence in a degree square similar to the African distribution map system used in Fig. 2.

SOUTH AMERICA



CHRYSOBALANACEAE

18. - Parinari Aubl. (1775)
Synthesis of plates 1-17

Table 5. New species and subspecies of Chrysobalanaceae described since the monograph of the family in 1972 (Prance, 1972a).

Species	Locality	Date of collection of the type
Couepia dolichopoda	Peru—Loreto	1972
Couepia edulis	Brazil—Amazonas	1971
Couepia glabra	Brazil—Amazonas	1971
Couepia marlenei	Brazil—Amazonas	1972
Hirtella arenosa	Brazil—Amazonas	1968
Hirtella conduplicata	Brazil—Amazonas	1973
Licania aracaensis	Brazil—Amazonas	1975
Licania chiriquiensis	Panama	1975
Licania furfuracea	Venezuela—Bolívar	1975
Licania jefensis	Panama	1969
Licania jimenezii	Surinam	1971
Licania marlenei	Brazil—Amazonas	1972
Licania montana	Venezuela—Lara	1975
Licania morii	Panama	1975
Licania octandra (Hoffmgg. ex R. & S.) Kuntze subsp. *grandifolia*	Brazil—Amazonas	1973
Licania pakaraimensis	Venezuela—Bolívar	1973
Licania stewardii	Brazil—Amazonas	1974
Licania cecidiophora	Peru—Loreto	1974
Licania sp. nov. 1	Ecuador	1969
Licania sp. nov. 2	Panama	1975
Licania sp. nov. 3	Brazil—Amazonas	1976
Licania sp. nov. 4	Colombia—Valle	1972
Licania sp. nov. 5	Panama	1972
Hirtella sp. nov. 1	Peru—Loreto	1976
Hirtella sp. nov. 2	Brazil—Amazonas	1976

true of a recent collection of J. Murça Pires in Amazonas, Brazil, from the recently discovered and isolated sandstone peak Serra Acará. The number of new species that are still being described from recent collections is indicative of the state of collecting. In 1972 I monographed the neotropical Chrysobalanaceae (Prance, 1972a). The monograph recognized 328 species in the 8 genera. Table 5 lists the 26 new species that I have described (or are ready to be described) in the five years since I completed the monograph. The new species amount to 7.93% of the original number of species. All except three of the new species are based on type collections made since 1970. Many other monographic, floristic, and descriptive works on the neotropical flora, especially from Panama southward, are adding species at a similar rate. The number of new species in Table 5 from the forests of Panama and from Amazonia points to two of the under-collected areas of the neotropics, although there are also many other places outside the main distribution range of the Chrysobalanaceae. In addition to these new species, large range extensions of several of the original 328 species have occurred. For example, *Licania affinis* Fritsch was reported as a species confined to the Guianas. It has recently been collected several times in Panama, adding another species to the increasing list of Guiana-Panama disjunctions reported in Gentry (1975). While this is a true disjunction, many other species previously thought to be of local distribution are now seen to have much wider

continuous distributions. For example, in Prance (1972a) I cited *Couepia longipendula* Pilger as endemic to the Manaus region of Amazonia. In 1973 I collected it over 1,200 km away on the Rio Curicuriari. It was then collected later in 1973 on the Rio Cunhua also over 1,000 km from Manaus to the southwest rather than northwest, showing that this species is actually quite widespread in Amazonia (Fig. 5).

Gentry (1978b) described a similar case in a species of *Siparuna* known only from Panama and western Ecuador, 1,500 km apart, but subsequently collected in Chocó in Colombia.

The number of species added to the Chrysobalanaceae and other groups in recent neotropical monographs is in marked contrast to the situation in African and Asian Chrysobalanaceae where few new species are being discovered. Jacobs (1974) cites a good example from the Malesian families monographed by Dr. P. W. Leenhouts (see also Leenhouts, 1976). The following additions to *Flora Malesiana* monographs have been made:

Burseraceae (108 species), additions after 14 years: 1;
Connaraceae (38 species), additions after 12 years: 0;
Dichapetalaceae (15 species), additions after 13 years: 0;
Goodeniaceae (8 species), additions after 13 years: 3.

The neotropics, as reflected in *Flora Neotropica* has a much less complete species inventory. In 1972 I monographed neotropical Dichapetalaceae (41 species; Prance, 1972b), since that date I have described 3 new species showing the same trend as for neotropical Chrysobalanaceae. However, this comparison of species between Malesia and the neotropics is further complicated by the differences in species concepts referred to earlier.

Although many new species are being added to the neotropical flora, also much synonymy is taking place. For example, in the monograph of Chrysobalanaceae (Prance, 1972a), where 75 new species were described, 76 names were placed in synonymy, giving an almost even result. Monographic treatments are finding many "regional" species. I suspect that in Lecythidaceae, which I am currently monographing with Dr. Scott Mori, the percentage of synonymy will be even higher since the last monograph by Reinhardt Knuth (1939). Knuth was a renowned splitter, and did not rectify the species described from several different regions under different names.

The dangers of such an incomplete inventory are obvious. Extreme caution must be taken with drawing biogeographic conclusions from plant distributions as we know them today. Some disjunctions are now well established and have logical historic bases, such as the climatic changes in the Pleistocene and post-Pleistocene (Haffer, 1969; Prance, 1973; Toledo, 1976); others are artifacts of a poor collection sample. Such disjunction as Panama-Guiana or Amazonia to the coastal forests of Bahia are well established. Lamentably, the destruction of the forest is proceeding at such a rate that we may never be able to put together the accurate distribution pattern of many neotropical plants.

Central America is one of the better known regions of the neotropics with

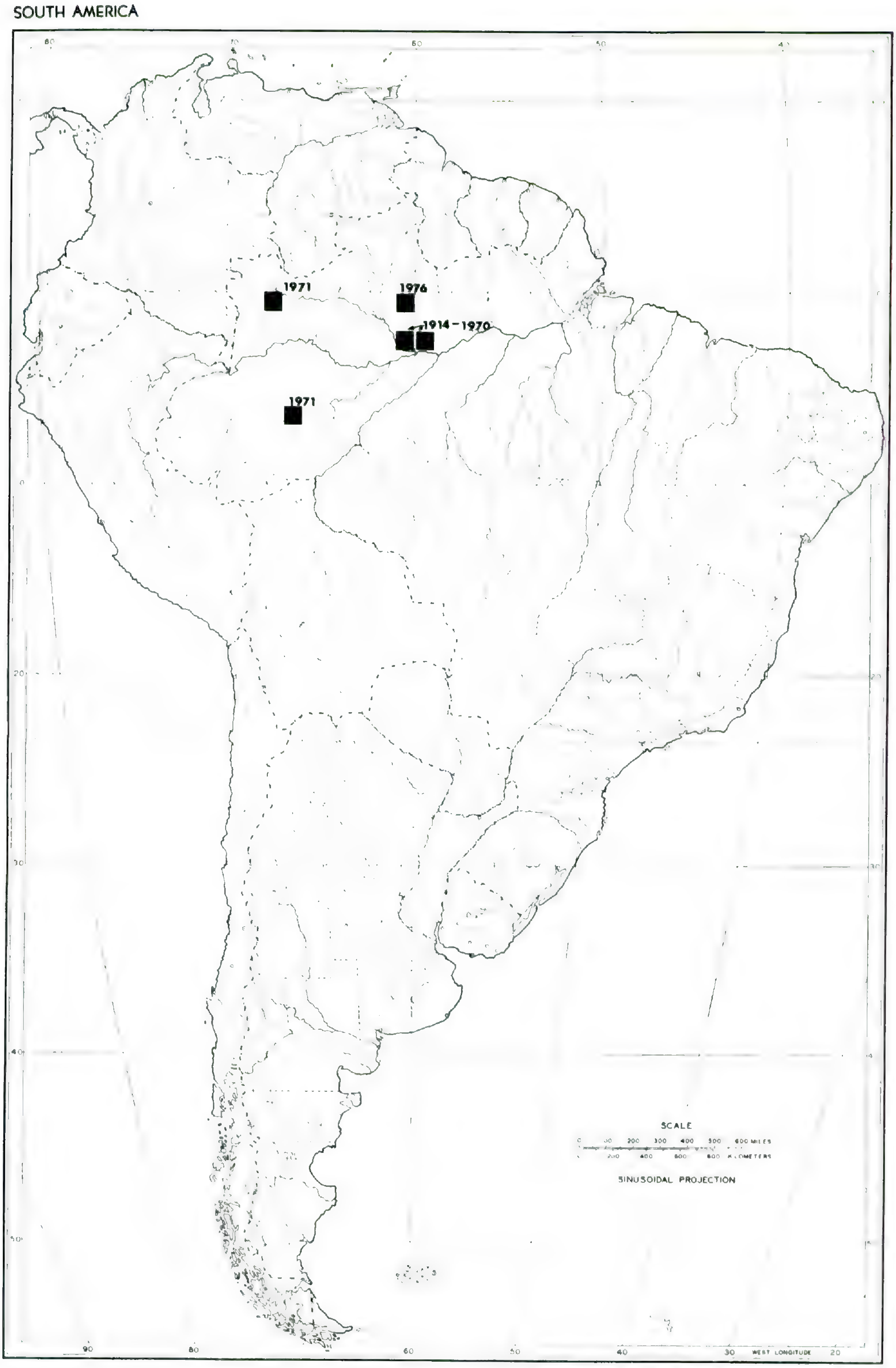


FIGURE 4. The distribution and range extension pattern of *Couepia longipendula* Pilger.

TABLE 6. Collecting density in Central America, data from Gentry (1978a) and other sources.

Country	No. of Species	No. of Collections	Surface Area (km^2)	Density Index (km^2)
Guatemala	8,000	80,000	108,880	0.73
Belize	3,000	25,000	22,272	1.12
El Salvador	2,500	8,000	21,392	0.37
Honduras	5,000	40,000	112,079	0.36
Nicaragua	5,000	5,000	129,990	0.038
Costa Rica	8,000	70,000	50,695	1.38
Panama	8,000	100,000	75,643	1.32

regional floras existing or in preparation in most countries. Work on the regional floras such as Guatemala, Costa Rica, and Panama has stimulated much botanical collection. Table 6 gives the approximate collecting density for the region. Only in two countries does it reach as high as 1.3 specimens per square kilometer. This may be compared to Table 3 where the lowest density for Malesia is Celebes with 19 specimens per square kilometer. Such a table for South America would be even lower than that of Central America. Holdridge (1976) discussed the reasons for the diversity of the Central American vegetation.

Perhaps the richest rain forest in the neotropics is that of Chocó, Colombia where annual rainfall is up to 10,000 mm (Lellinger & de la Sota, 1972). Only about 8,000 collections have been made from this area, first by Cuatrecasas and more recently by Gentry and Forero. It is certainly one of the most important and most interesting areas in the tropics for future collection. Colombia as a whole has the richest flora in South America with perhaps half the species of the neotropical flora occurring within her territory, 45,000 species (50,000 according to Schultes, 1951). Colombia as a country is still poorly collected and many areas rich in endemism such as Sierra de la Macarena and Sierra Nevada de Santa Marta are poorly known botanically.

Venezuela is relatively well explored botanically in comparison to many other countries of South America, yet Steyermark (1974) stated that "less than 2% of Venezuela has been explored botanically." Maguire (1970) estimated that more than 75% of the flora of the Guyana highlands is endemic. With the high endemism from mountain top to mountain top in that region, even the intensive expeditions of Maguire, Steyermark, and other collaborators has just begun to inventory the flora of the sandstone mountain tops. The large state of Apure in Venezuela offers diverse habitats, savannas, lakes, rivers and rain forests, rarely visited by botanists.

In the Guianas, French Guiana remains the least explored and is in need of much more intensive fieldwork.

Svenson (1945) stated that "Ecuador is botanically one of the least known, though one of the richest countries in South America." This is still true today, although the Swedish-based *Flora of Ecuador* project has stimulated much more collecting activity in recent years. This has concentrated on the highland areas, leaving the Amazonian part of Ecuador still very poorly known.

Peru also offers a wide range of plant habitats, from arid desert regions to the humid tropical forest of her Amazonian territory. Despite the long history of collection in Peru, it is still poorly known botanically. The *Flora of Peru* initiated by Macbride in 1936 has recently been reactivated as a cooperative Field Museum-Missouri Botanical Garden project. This has stimulated more collections in recent years, particularly from the poorly collected Amazonian region.

Brazil, the largest country in South America, has a long history of botany, and a great diversity of vegetation. With an area of 8,511,965 km^2, the collecting density of the country is certainly well under 1 specimen per square kilometer. National herbaria have about 2 million specimens. Some of the poorly collected areas of Brazil include the state of Acre, Serra Pacaás Novas in Rondônia, the forests of northern Mato Grosso and Serra Cachimbo in Amazonia. Besides the Amazonian region there are many other neglected areas of Brazil such as the coastal forest of Bahia and Espiríto Santo and some parts of the arid caatinga region.

In January 1976 Brazil initiated an ambitious program called *Programa Flora.* This program plans to make a detailed inventory of Brazil's vegetation by collecting programs and by the preparation of a computerized label data bank of Brazilian herbaria. The program is divided into five regional projects and *Projeto Flora Amazônica* has already begun. Arrangements for North American participation in the collecting program have been made and collecting will start in the fall of 1977.

Bolivia is probably the least collected of all South American countries. Little collecting has been carried out since the time of the summary of collections from Bolivia by Herzog (1923: 1–4). The lack of a strong national botanical work in Bolivia has also hampered fieldwork by foreigners. There is a great need for collections from all over Bolivia.

Paraguay, which lies geographically half within the tropics, is another poorly collected country where only about 30 collectors have worked extensively. Argentinian botanists have visited Paraguay and made important collections there. There is very little primary vegetation left in Paraguay.

The Caribbean islands of the Antilles have a flora of 12,000–15,000 species (Howard, 1977). The islands, which stretch over 1,700 miles east to west and 1,200 miles north to south, have many local endemics. For example León and Alain estimated that almost 50% of the 6,000 species of Cuba are endemic, and Hispaniola has 33% endemism in its flora of 5,000 species (Alain, pers. comm.). The history of floristic work has been a one-island approach which has led to many species being described from several islands, and more island "endemics" are being reduced than new species described. One of the needs of Caribbean botany is a monographic approach to compare elements of its flora with South and Central America and to calculate the true percentage of endemism. Howard (1977) has noted that "plant life of the Caribbean Islands cannot be regarded as unknown or needing immediate study or a massive collecting program." The area has been well collected in comparison to Latin America.

There is, however, a need for any of the experimental type collections listed in the next section. Howard (1977) lists many examples of environmental de-

TABLE 7. The most recent country or regional floras of Latin America.

Country	Status	Reference
Guatemala	(almost complete)	Standley & Steyermark (1958–)
Belize	Annotated checklist	Standley & Record (1936)
El Salvador	Annotated checklist	Standley & Calderón (1925)
Honduras	Various regional floras and checklists	Standley (1930, 1931)
Nicaragua	Initiating Flora, none published	
Costa Rica	Flora in progress	Burger (1971–)
Panama	Flora nearing completion	Woodson & Schery (1943–)
	Flora of Canal Zone	Standley (1928)
Colombia	Generic Flora initiated, none published	
	Flora of the State of Cundinamarca in progress	Pinto-Escobar (1966–)
Venezuela	Flora in progress	Lasser (1968–)
Guyana	No flora	
Surinam	Flora under revision	Pulle (1932–)
French Guiana	Compiled incomplete Flora, no modern Flora	Lemée (1953)
Ecuador	Flora in Progress (6 families published)	Harling & Sparre (1973–)
Peru	Flora reactivated, in progress	Macbride (1936–)
Brazil	No modern Flora since Martius	Segadas-Vianna (1965–)
	Various local floras e.g. Santa Catarina, Restingas, etc.	Reitz (1965–) Hoehne (1940–)
Bolivia	No Flora	
Paraguay	No Flora	

struction in the Caribbean, and, as elsewhere, further collecting data is needed for conservation information.

Floras exist for many of the larger islands, for example, Cuba (León & Alain, 1946–1969), Puerto Rico (Britton & Wilson, 1923–1930), Jamaica (Adams, 1972; Fawcett & Rendle, 1910–1936), and that of Hispaniola is in preparation by Alain.

In spite of the better collecting status of the region, there are still novelties being found in the Caribbean, for example, Alain recently found a new species of the previously South American genus *Talisia* in Santo Domingo (Alain, pers. comm.). Some of the smaller islands of the lesser Antilles have been overlooked.

Table 7 gives a list of the most important local floras in the neotropics. The collecting for the floras has done much to stimulate the inventory of the region, but most of the floras are based on inadequate specimen samples and consequently new species and extension of ranges must be added to the floras of each country. For example, the earlier family treatments of the *Flora of Panama* (Woodson & Schery 1943) are very inadequate in their species coverage and nomenclature. The recent exploration of the moist forests of Panama has added many elements to the flora. Another result of such an emphasis on regional floras has been the description of many species several times in the various regional floras. Even Paul Standley (1928), known as a "splitter," commented that "in tropical America . . . the flora has been studied from isolated centers with little regard for the species accepted at other centers, but with the assumption that each area is floristically distinct. Correlation through monographic work, covering a group throughout its range, will reduce the species that have been multiplied unnecessarily."

TABLE 8. Number of species described in *Flora Neotropica* monographs.

Volume	Author	Group	No. of Species
A. Flowering Plants			
1	Cowan (1968)	*Swartzia*	127
2	Cuatrecasas (1970)	Brunelliaceae	50
7	Berg (1972)	Olmedieae-Brosimeae	68
8	Maas (1972)	Costoideae	41
9	Prance (1972a)	Chrysobalanaceae	328
10	Prance (1972b)	Dichapetalaceae	39
11	Prance (1972c)	Rhabdodendraceae	3
12	Prance & Silva (1973)	Caryocaraceae	23
13	Rogers & Appan (1973)	*Manihot/Manihotoides*	99
14a	Smith & Downs (1974)	Pitcairnioideae	731
14b	Smith & Downs (1977)	Tillandsioideae	815
15	Morley (1976)	Memecyleae	81
18	Maas (1977)	Zingiberoideae	61
		TOTAL	2,466
B. Fungi			
3	Singer (1970a)	Omphalinae	52
4	Singer (1970b)	Phaeocollybia	4
5	Singer (1970c)	Strobilomycetaceae	13
6	Lowy (1971)	Tremellales	148
16	Farr (1976)	Myxomycetes	280
17	Singer (1976)	Marasmieae	322
		TOTAL	819

Recent monographic work has shown the words of Standley to be true, and most neotropical monographs include a considerable amount of synonymy, but at the same time also include a large number of new species.

Another stimulus to collecting in the neotropics is the *Flora Neotropica* monograph series initiated in 1964. Table 8 gives a list of the monographs published to date: 2,466 species or 2.74% of the estimated total of 90,000 flowering plants have been treated, and 819 species or 1.64% of the 50,000 fungi have been treated. Since the series also includes ferns, bryophytes, and algae, the task to be completed is enormous. Already new collections are outdating the existing treatments, see, for example, Table 5, the Chrysobalanaceae added since 1972. Maas (1977) contains a supplement to Maas (1972) which adds many new data.

THE FUTURE INVENTORY

In summary, Africa is the best collected continent of the tropics and is closely followed by Asia and Malesia. In these areas a basic inventory including most species exists, but the sample size of many species is still inadequate for a true understanding of their biology and ecology. In the neotropics the basic inventory is still underway, and many new species are still being found. There are many areas of South America still to be explored botanically. However, collecting should not now be slowed down anywhere in the tropics. A different emphasis is needed now to provide an adequate experimental sample. Some of the foci

for future collecting are outlined below, and these correspond with the needs of a more experimental approach to tropical taxonomy. Although herbarium inventory is still taking place in many areas, the experimental methods can often be carried out at the same time. For example, it is easy for any collector to carry fixatives and collect bud material for the study of chromosome numbers.

Throughout the tropics many species are known from incomplete material. Future collecting should focus on previously inadequately collected material such as the fruits of many tall forest trees, and collections should be accompanied by good field data and notes on dispersal where possible. Jacobs (1976) pointed out that lianas are poorly collected and gave a succinct summary of collecting problems in lianas. The large fleshy, monocotyledons such as Zingiberaceae (see Burtt, 1976), Musaceae, and Araceae are poorly collected, and pickled flowers are essential for adequate study. Much more liquid preserved material should be collected and distributed to specialists. At the outset of my work on Lecythidaceae it was necessary to obtain a large collection of preserved flowers over a period of several years before the complicated androecium structure of the large fleshy flowers could be interpreted. Other groups that are poorly collected include tropical macrophytes, bamboos, palms, and *Utricularia* (see Taylor, 1977, for collecting techniques in *Utricularia*).

Van Steenis (1977) made an important plea to tropical collectors to improve their field data. He pointed to the need for further label data on color, scent, size, texture, structure, and habit of specimens, for liquid material, and for black-and-white photographs of habit and habitat. As studies on floral biology, phytogeography, and evolution in the tropics increase these are needed. It is often better to collect fewer numbers but to document them well.

Economic plants have often been neglected by taxonomist collectors who have the habit of leaving such things to economic botanists, agriculturists, or foresters. This has resulted in inadequate sampling of many of the most important economic plants and even their wild relatives. The contrary has occurred in some tropical areas where the local herbarium is a Forestry Herbarium. Collecting was concentrated on forest trees and "noneconomic" plants like forest herbs and lianas have been neglected, for example, in North Borneo, Surinam, and French Guiana where forest herbaria are the most active botanical institutes.

Plants of secondary vegetation have always been neglected as "inferior cousins" of the primary forest. Some secondary areas have an extremely rich and interesting flora, and they should also be further collected. For example, many of the hard-to-collect forest lianas in Bignoniaceae, Malpighiaceae and Menispermaceae occur abundantly in the secondary forest areas of the neotropics. A survey by Rodrigues (unpublished data) found 374 species in 63 families on an area of 3,500 m^2 of secondary forest near Manaus.

Various authors have drawn attention to the importance of secondary forest in conservation of primary areas. Thus, use of secondary areas for plantations can often relieve pressure on primary areas (Budowski, 1977). Secondary forest also played an important role in the evolution of the tropical flora (Gómez-Pompa, 1972). It is, therefore, most important that we make a better inventory of secondary areas in the tropics.

General collecting is important and has really provided the basic inventory of the tropical vegetation. However, a specialist in any family finds far more interesting things about his group than the general collector. The specialist soon learns to recognize his group from the diversity of the forest, and field studies by specialists have contributed many of the interesting results from the tropical forest. I have been accompanied by many specialists on my botanical expeditions and have often been impressed at their ability to find their groups, and the representation of any family in our collections always increases when there is a specialist present. There is much in favor of taxonomic focusing in collection. A general collector who concentrates on certain groups will also produce interesting collections.

Another important aspect for tropical forest areas is the concentration on a small area over an extended period. This is best done by resident botanists and can be highly rewarding, from both a taxonomic and ecological point of view. For example the selection of one hectare of forest for study in a relatively well-known area near Manaus, Brazil yielded many interesting results, including at least two new species from the 236 tree species on the hectare (Prance et al., 1976).

The detailed botanical study of Barro Colorado Island in Panama (Croat, in press), was based on much fieldwork and treats 1,400 species from an area of 14.8 km^2. This study has also enhanced many other interdisciplinary studies and is a good example of the usefulness and importance of minifloras and treatments and inventories of small areas of the tropical forest. An area where the individual trees have been identified soon becomes the focus of many other studies apart from the original botanical inventory. Often the biggest problem facing other tropical biologists is the lack of such well-inventoried areas for their research. When we had inventoried the hectare of forest near Manaus, we were soon followed by entomologists, soil zoologists, and mycorrhiza specialists who could link their work to an accurate botanical inventory. Too many detailed tropical forest inventories in the past were carried out by foresters who relied on local names and did not collect enough herbarium specimens to document their inventories. There is a need for further well-documented inventories of small areas from throughout tropical forests. This type of inventory is quite as important as general collecting and often yields data of great use for conservation, as well as ecology and other disciplines. It is one of the best ways to encourage interdisciplinary research. Much of the interesting work that has come from the Organization for Tropical Studies in Costa Rica is the result of concentration on small, well-inventoried areas of forest.

Inventory must not be isolated from the other subjects under discussion in this symposium. It is significant that other speakers are covering animal-plant interactions, tropical ecosystems, and integrative approaches to the study of plant structure. Future collectors need to be more aware of the research being carried on in these and other fields, and to be ready to contribute data. The lack of pollinator data in the tropics is enormous, and both the general collector and the specialist collector can contribute much to pollination ecology by making a few observations on flower visitors, scent, etc.

Inventory in the tropics does not just include the collection of herbarium specimens which I have emphasized in this paper. It includes inventory of pollination mechanisms, other insect-plant relationships, phenology, mycorrhiza, types of photosynthesis, nitrogen fixing bacteria, chromosome numbers and morphology (Raven, 1975), self-incompatibility mechanisms (Bawa, 1974; Bawa & Opler, 1975), hybridization—of which we know virtually nothing in the tropics (Raven, 1976c), and many other aspects which are summed up by Farnworth & Golley (1974). Let us remember the words of Merxmüller (1970) in reference to biosystematic work in the tropics, "A conservative today who would work on insufficient materials only, would soon be a laughingstock," and try to improve the situation rapidly.

One of the most striking facts about the tropics is that the vast majority of specimens are deposited in herbaria in temperate regions. The history of settlement and development has dictated the distribution of specimens, and this is now a major problem for the development of systematics and conservation in the tropics. There are very few major herbaria anywhere in the tropics, and they can easily be enumerated on two hands. They include Bogor and Singapore in Malesia; Calcutta in India; The East African Herbarium in Nairobi; The Forest Herbarium in Ibadan, Nigeria; and the Jardim Botânico and Museu Nacional in Rio de Janeiro. There are of course fortunately a large number of smaller tropical herbaria that play an important local role; for example, there are at least 49 herbaria in Brazil alone, 16 in Colombia, etc. (see Table 9). Their work is hampered by the lack of type specimens and literature. Not only are the specimens deposited in Europe and North America, but also the best literature about an area is often in a foreign language such as English or German.

This lack of resources has also been accompanied by a lack of trained personnel in tropical countries which has also hampered the progress of inventory. These facts, coupled with the increase of nationalism, have led to the implementation of strict rules to govern collecting activity by foreigners with the result that there are some tropical areas where it is impossible for foreigners to collect at present.

In order to complete the inventory of the tropics it is necessary to stimulate more training of local resident botanists (Prance, 1975), to deposit properly identified material in all tropical herbaria equipped to house them, and to publish in local journals in the countries where we are working. This will not only have an effect on the standard of botany in those countries but also contribute significantly to conservation. The enthusiasm and concern for conservation displayed by botany and ecology students in our training program in Manaus, Brazil, is an unforgettable experience. These young biologists will be a powerful force for conservation in a few years' time. The issue of conservation is even more sensitive than collecting, and it cannot be accomplished by foreigners without much support from within the host country.

In order to progress in the future inventory and conservation of the plant resources of the tropics, botanists must adhere more strictly to the excellent guidelines agreed upon by many major United States Research Institutions (Hairston, 1970).

TABLE 9. A summary of South American herbaria and areas covered.

Country	Number of Herbaria	Total No. of Herbarium Specimens	Area of Country (km^2)
Colombia	16	260,000	1,138,914
Venezuela	5	190,000	912,050
Guyana	2	30,000	214,969
Surinam	1	16,000	163,265
French Guiana	1	13,500	91,000
Ecuador	4	7,500	283,561
Peru	6	275,000	1,285,216
Brazil	49	2,000,000	8,511,965
Bolivia	1	1,000	1,098,581
Paraguay	1	1,000	406,752
Uruguay	3	115,000	177,508
Chile	4	160,000	756,945
Argentina	22	3,000,000	2,776,889
TOTALS	115	6,068,500	17,817,615
U.S.A. (1974)	1,127	45,811,608	9,360,882

Inventory of the tropics is not nearly complete, yet destruction of their natural ecosystems continues not only unabated, but at a faster rate than inventory. There is an urgent need to accelerate the process of inventory and at the same time to encourage alternatives that will buy time for us by delaying the destruction of the world's richest biome. The more knowledge we gather about the ecosystem the better the possibility that we can use it on a sustained-yield basis. In the meantime we should do all we can to encourage some of the alternatives: the exploitation of seasonal forests (Budowski, 1976; Goodland & Irwin, 1977), floodplain forests (Goodland & Irwin, 1975; Prance, in press), of secondary forest (Budowski, 1975; Farnworth & Golley, 1974), and better distribution of food produced in temperate regions. Clearly there is still an enormous challenge ahead of us in the task of a complete tropical inventory.

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PLANT MORPHOLOGY AND ANATOMY IN THE TROPICS—THE NEED FOR INTEGRATED APPROACHES

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Plant morphology, like justice, must not only be done, it must be seen to be done. It must be done because it is foundational to many major disciplines—systematics, ecology, and plant physiology. Similarly plant morphology is initially an observational discipline; the pun is intentional because I want to speak from the point of view of the research worker who needs direct access to his material and the opportunity to "see" the functional significance of form and structure which is investigated.

Modern high speed travel has made easy the traditional process of what may be called "body-snatching," i.e., the initial collection of fluid-preserved or dried materials which the plant morphologist uses for much of his work. Body-snatching has contributed the largest part to our understanding of tropical plants and needs to be actively encouraged because it provides the initial comparative background to any biological enquiry. Here I want to emphasize the need for elaboration of or departure from this classical approach in what I will call integrated studies of biological features of tropical plants. Integration here has a dual meaning, it refers to the need to combine elements of disparate disciplines—anatomy, physiology, biochemistry, ecology, and plant-animal interactions—but also emphasizes an approach which recognizes the organism itself as an integrated entity so that something of its total biology is revealed.

Corypha provides a simple but dramatic example of a tropical plant consisting of a single hapaxanthic module in which the switch from vegetative to sexual growth is complete, with marked contrast between the massive unbranched vegetative axis to the highly branched determinate inflorescence, with resulting proliferation of another generation of meristems. Here vegetative and reproductive phases are sharply segregated, but they must occur in the right sequence and at the right time. A striking example, which illustrates the way in which a branched organism can function as an integrated physiological unit is provided by *Cerberiopsis candelabrum* (Apocynaceae), a small tree in New Caledonia which is monocarpic (Veillon, 1971). Here a tree that is architecturally precisely branched in the initial vegetative stage eventually shows synchronous flowering and fruiting which ends in its death—rather like many annual weeds. A second species, *C. comptonii*, a treelet with smaller leaves, is not monocarpic. This genus therefore provides material for the study of a biological problem which may be approached comparatively but requires access to field populations. The plants under consideration are large and can only be represented in herbaria by fragments. An appreciation of the adaptive significance of this life style would draw on several disciplines—anatomy, physiology, and reproductive biology.

It has to be appreciated that modern travel in the tropics is easy and a

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relatively inexpensive research item, compared with the many requirements of modern scientific investigation such as equipment, chemical analysis, technical support, and storage facilities. Also, common organisms which are easily accessible need prime consideration, there is no initial need for expeditions to remote areas. We are not looking here necessarily for new approaches; great scope is provided simply by the enormous diversity of tropical plants. The greatest emphasis needs to be given to the study of the morphology and anatomy of woody plants since trees dominate many tropical ecosystems with great floristic richness. This diversity is readily documented and quantified (e.g., Poore, 1968; Ashton, 1969; Rollet, 1974; Hallé et al., 1978). Here I attempt to demonstrate by means of a few selected examples the ways in which the scope of classical plant morphology and anatomy can be broadened by emphasizing functional relations, integrating the approaches of specialists in several fields, and adopting a holistic view of the plant. The object is to illustrate examples which in turn can provide guidelines.

PRIMARY MERISTEMS

From the point of view of the population biologist the "individual" in a tropical forest may or may not be easily recognizable for demographic purposes since clonal propagation of plants makes possible a distinction between "ramet" and "genet," to use the terms of Harper & White (1974). A useful starting point for the morphologist is to consider primary meristems as the unit making up the forest, following the suggestion of Oldeman (1974). It then becomes possible to study the ways in which primary meristems originate, function, are protected, interact with each other, and eventually die, adding a time scale and dynamic considerations to classical plant morphology. Of course, this approach is only one of many which could be adopted, but it seems of fundamental biological significance.

In this approach one can make the useful distinction between seed-originating meristems (i.e., via sexual reproduction) and vegetative meristems (both of which may be either latent or active). The production of seed-originated meristems centers on floral biology, itself an integrated discipline which will be mentioned later. Activated seed meristems are found in germinating seeds and the subject is resplendent with morphological detail (e.g., Burger, 1972; Duke, 1969; Ng, 1975, 1978) which now requires an extension into functional analysis. Ecology, physiology (e.g. of dormancy), population biology, and morphology are all interdependent at this critical phase, and yet there are few studies which attempt a functional explanation of seedling characters. Jackson (1974), to some extent, succeeded in his recognition of cryptogeal germination because he added field observations to his morphological data. The classical distinction between hypogeal and epigeal germination (or cryptocotylar and phanerocotylar, dependent on semantic tastes; Duke (1969)—which Ng (1978) has shown to be too simplistic to accommodate tropical diversity—presents in itself two contrasted biological life styles still awaiting exploration, and shows interesting analogies with contrasted branching processes (prolepsis and syllepsis), as pointed out by Hallé et al. (1978).

BRANCHING

The vegetative meristems are of prime concern to the plant morphologist since they originate the structures in which he is interested. For active primary meristems, interaction between them within the individual tree have been outlined by Hallé & Oldeman (1970) who have provided a conceptual framework which now makes it possible to talk about tree form in a comprehensible way. This foundation can be built upon by the morphologist. An important developmental approach is to study ways in which vegetative meristems multiply, as in the study of branching patterns. The element of discovery which is still possible in descriptive tropical plant morphology is illustrated by the recent demonstration of equal dichotomy of vegetative apical meristems in a number of angiosperms (e.g., Boke, 1976; Fisher, 1976, Tomlinson, 1971; Tomlinson & Posluszny, 1977). That this is not a factor of any direct evolutionary significance is easily argued, especially with recent methods of mathematical analysis of branching patterns to provide a much needed background of quantification and theory (especially Oohata & Shidei, 1971). Equal dichotomy permits only a minimal value for a bifurcation ratio, whereas high bifurcation ratios seem adaptive in many ecological circumstances (Whitney, 1976). It seems reasonable to assume that the early development of highly controlled *axillary* branching in vascular plants has made possible the elaborated vegetative body of modern angiospermous trees (and, of course, other life forms), a statement which is little more than axiomatic (Tomlinson, 1978). A mathematical analysis of branch form provides a useful conceptual framework. It is still interesting that gymnosperms appear to lack any mechanism for generating shoots with distichous phyllotaxis and so have lost one degree of freedom much exploited by the angiosperms in their branch architecture, especially the plagiotropic shoots of many monocotyledons.

Axis differentiation in woody plants, which is a major parameter of Hallé and Oldeman's system, in the most specialized situation has a simple morphological basis since shoots with contrasted orientation can have different phyllotaxis—spiral in orthotropic, distichous in plagiotropic. The ability of the same genotype to support such contrasted primary meristems which operate contemporaneously provides scope for extended morphogenetic analysis. A comparable example is found in shoots with phase change from one type of orientation to the other during the activity of a single meristem. The best examples are provided by rhizomatous herbs where foliar dimorphism associated with sympodial growth is common, as in many Zingiberales.

Syllepsis, as contrasted with prolepsis (using these terms in the expanded definition given by Tomlinson & Gill, 1973) provides the most convincing demonstration of how limiting of elementary concepts temperate-based botany may be, since syllepsis (development of a lateral axis contemporaneous with its parent) is common only in tropical woody plants and is little developed in north temperate woody plants because lateral axes here usually undergo a period of dormancy before extension (i.e., show prolepsis). And yet these terms are needed to describe two fundamentally contrasted conditions. Why syllepsis should be so characteristic of tropical trees still awaits an ecological explanation, but recog-

nition of this simple developmental distinction opens up numerous opportunities for comparative anatomy.

The combination of anatomy and translocation physiology which integrates this dynamic aspect of shoot morphology is likely to be found in the recent demonstration by Zimmermann (1978a, 1978b) of the unequal distribution of hydraulic conductivities in trees. In particular, there are pronounced constrictions at every branch-trunk junction. This must have an anatomical basis and perhaps even provide a causal explanation for continued apical control of one type of shoot over another. Since prolepsis and syllepsis may determine differences in axis orientation in many trees, there is the possibility of analyzing continuity between dynamic morphology and subsequent function in a novel way. The anatomy of branch insertion may thus become as important in understanding the ecological significance of form in woody plants, as has comparative study of the stem-node-leaf continuum provided material for systematic and evolutionary analysis (Howard, 1974).

Secondary changes in axis orientation depending on differences in vigor that suggest hormonal mechanisms of control are important in a number of tropical trees (Koriba's model). Reaction anatomy as a functional mechanism in the organization of woody plants remains little explored, but is a topic likely to be a rich source of information in the future (cf. Fisher, 1978; Tomlinson, 1978).

BUD BIOLOGY

The persistence or otherwise of vegetative meristems in plants depends not only on genetic organization but also, as determined by ecological accident, on the efficiency with which shoots and their associated primordia are protected, as from predators, drought, or excess heat. Devices which can be interpreted as protective are often mechanical and conspicuous, but biochemical devices are probably equally if not more common. Here developmental anatomy, morphology, and organic chemistry need to be integrated. For larger shoots, size alone, combined with the rigidity of mature appendages, may be sufficient, as in woody monocotyledons. Many palms have efficient supplementary organs, like spines and mechanical leaf bases, as befits plants which are vulnerable because they may possess a single apical meristem incapable of vegetative branching (Uhl & Moore, 1973; Tomlinson, 1962). *Pandanus* is typically protected by serrated leaf margins. The morphological diversity of buds in dicotyledonous woody plants is well known since they so often offer useful diagnostic field characters, but the only extensive summary refers largely to temperate species (Lubbock, 1899). Although the mechanical efficiency of enveloping stipules, leaf bases, and petioles is very evident, this alone does not explain why buds seem often to be the last organs to be attacked by insect predators—or why buds can survive in the absence of mechanical sheaths. The "biology of buds" is a little explored field where the morphologist will need the assistance of biochemists in order to make progress, I believe. The concept of plant apparency (Feeny, 1976) has to be put in a morphological context, with the relative vulnerability of different parts contrasted.

In making very general surveys of tropical plants one can, for example, dis-

tinguish "wet" buds from "dry" buds, the former characterized by some fluid or resinous secretion. Wet buds commonly are associated with stipular devices which support colleters or equivalent glands, as in Rubiaceae, Rhizophoraceae, and Polygonaceae. Here the stipule may simply provide the cavity which accommodates the fluid secretion. Even where the stipules are small ("vestigial" to some comparative anatomists), as in many Euphorbiaceae, Ulmaceae, Celastraceae, and Elaeocarpaceae, they are likely to perform a vital function, since they can mature before associated leaf primordia, and their biochemical specialization may be indicated by their high tannin content, an observable microscopic feature. In other buds which lack stipules there is no such division of labor, and the leaf primordia themselves are tanniniferous. Secretions which dry as conspicuous, resinous or varnishlike coatings of unknown chemical composition, but probably polysaccharides, are common in tropical woody plants—they may make the bud distasteful, resistant to drying, reflect damaging wave-lengths, and mechanically impede chewing insects. This exuded material is something that production ecologists should not overlook, since it is often exfoliated in considerable quantities. In *Ceriops* (Rhizophoraceae) between 25 and 40% of the dry weight of the bud is made up of this varnish. Initially it simply fills the quite considerable free space between stipules and leaf primordia—at this stage it is a close packing device which is related to the periodicity of growth extension; subsequently the varnish becomes a casing to the expanding leaves and internodes, with unknown biological properties; finally it sloughs off. The material has not yet been analyzed biochemically, but a large amount is produced and lost each time a leaf pair expands.

A possible biological function for bud secretions in other Rhizophoraceae has been shown recently by Richard Primack, in Queensland. He found that a galactose-rich exudation served as a bird-attracting device in *Rhizophora stylosa*, since nectar-feeding birds would lick this sweet fluid which is apparently produced by the nonvasculated stipular glands (colleters). Such birds are likely to also pick off insects, this grooming being of presumed benefit to *Rhizophora*. Here, therefore, initial studies on the anatomy of colleters have an extension into biochemistry and plant-animal interactions.

The term "naked bud," which is sometimes used to describe meristems without specialized mechanical protection, is not particularly appropriate because leaf primordia at an arrested state of development are frequently associated with a specialized but ephemeral indumentum, or with latexlike secretions. The initial need is not for elaborate categorization, but for the examination of specific case histories with the concept of the bud as a biological unit given prime consideration.

Emphasis must be given to the construction of buds in relation to the method of shoot extension, i.e., whether rhythmic, continuous, or intermittent (without regular periodicity). In many tropical woody plants a stipular organ can serve as an "instant" bud scale, the shoot ceasing to extend without reference to any endogenous rhythm but still retaining a protective cap. The relation between stipule position and the region of extension is of interest. In most examples internodal extension occurs beyond the level of stipule insertion, but in some

Cunoniaceae, a family characterized by well-developed interpetiolar stipules, the stipule pair is carried up with the bud by extension of the internode below it. The idea that bud morphology is a dynamic and not a passive subject is one that can be encouraged by the comparative study of the wide diversity of plants available in the tropics.

Internal secretions, most noticeable in those numerous tropical families with latex, often of commercial importance (Apocynaceae, Asclepiadaceae, Moraceae, Sapotaceae, and Euphorbiaceae) provide an area for integrated studies combining anatomy, developmental morphology, chemistry, and adaptive biology. This can be illustrated in a spectacular way by the recent report that the New Caledonian endemic *Sebertia acuminata* (Sapotaceae) accumulates as much as 25% by dry weight of the heavy metal nickel in its latex (Jaffré et al., 1976). This is undoubtedly an exceptional case, but it does indicate part of the mechanism whereby a plant can tolerate soils with a high content of heavy metals and shows an interesting correlation between plant anatomy and mineral nutrition. Both the distribution of laticifers within this plant, and the distribution of heavy metals and inorganic compounds in laticiferous organisms offer themselves as subjects for study. It is known that nickel accumulators are not necessarily laticiferous (Brooks et al., 1974), but where does nickel accumulate in plants of high nickel content? Electron microprobe analysis of appropriate organisms could usefully integrate ecology, anatomy, and chemistry. Of interest is the way in which herbarium specimens have been used in this research (Brooks et al., 1977) showing the lasting value of "snatched bodies."

FLORAL BIOLOGY

This area represents perhaps the most profitable one for integrative studies, and a number of recent workers have combined comparative and developmental anatomy with field study of flower visitors and pollination biology. In part this is a response to Carlquist's (1969) critique of the general subject of floral anatomy, but much reflects the increasing field orientation of modern morphologists. The most extended study of this kind is that of Uhl & Moore (1977) on palms in which a syndrome of characters is described in detail for inflorescence and flower patterns in six examples representing two anemophilous and four different entomophilous modes of pollination. This study has as its basis one of the most complete systematic and anatomical backgrounds known for any family of tropical plants (Moore, 1973) and should serve as a model for future studies. It extends the concept of "protection" of meristems to ovules and pollen, but backward in time to the vegetative meristems which ultimately produce them, via the often elaborate inflorescence to the floral envelopes and mechanisms which assist in fertilization and then anticipates the later processes which contribute to the formation of seeds and fruits. We therefore add a time scale and additional biological dimensions to comparative studies which began with studies of floral vasculature.

Reproduction "strategy" may even have to be integrated with photosynthetic "strategy" since position of flowers or inflorescences can determine the architectural model in Hallé and Oldeman's system. Of interest are those contrasted

examples where the presence of terminal versus lateral inflorescences, resulting in determinate or indeterminate axes, in turn produces an architecture which is the morphological analogue of monolayer and multilayer, to use the terminology of Horn (1971) for probable contrasted photosynthetic strategies in trees. This kind of example shows how emphasis of a particular dynamic aspect of one phase in the life cycle of a plant inevitably leads from one topic to another, such is the nature of an organism as an integrated whole.

A field-orientated approach to comparative morphology which illuminates floral structure is shown by recent studies on the mangrove Rhizophoraceae (Tomlinson et al., in preparation). This involves 4 genera and about 20 species with a comparable vegetative morphology (architecture, bud morphology) and habit (marine swamps) but with evident niche diversification shown by quite complex ecological zonation, which is reflected morphologically in diversity of aerial root development. A common floral plan is involved, indicative of a common evolutionary ancestry but with immediately obvious variation in such features as inflorescence branching, flower size, orientation, and number of parts. A dominant feature is the dehiscence of stamens within the unopened flower. Functionally at least 6 types of floral mechanism can be recognized according to the way parts behave in relation to pollen vectors. These types transcend taxonomic boundaries because a single genus can include contrasted mechanisms (*Ceriops*) or be adapted to different visitors (*Bruguiera*). An unusual mechanism which is the result of considerable developmental complexity is a catapult release of pollen, with stamens initially enclosed by petals in a spring device triggered by a flower visitor. Despite this common piece of engineering, flowers are visited more or less exclusively by birds on the one hand, insects on the other, with further specialization according to the type of insect—moth versus butterfly, for example.

Extending these observations in a comparative way, considerable circumstantial evidence accrues that the genus *Rhizophora* is an exceptional component of mangrove communities because it is wind pollinated. This may be one reason for its evident ecological success and is the basis for an understanding of genetic aspects of its species interrelationships which are suggested by certain taxonomic peculiarities in the genus. This step-by-step development of our understanding of this widespread and important genus began with simple curiosity about its morphology and anatomy. The essential ingredients in the success of this continuing research have been repeated access to natural populations and collaborative work with other specialists—field ecologists, population biologists, and biochemists and attempts to understand different components in a biological continuum.

Conclusions

The examples chosen are few and refer to a restricted field. Similar approaches to different topics could have been adopted. Instead of primary meristems, the secondary meristems of tropical woody plants could have provided a focal point. Knowledge of fluctuations in the activity of vascular cambia in tropical trees is very scant and we largely lack the important ecological param-

eter this provides in temperate trees—the ability of an observer to determine tree age quite accurately is missing in tropical forests.

The structure and development of root systems in tropical plants is little explored, especially the interaction between roots and soil microorganisms (cf. Janos, 1975). For this topic, even descriptive morphology is at a very elementary stage.

One particularly useful field which needs expanding is the study of the morphology and anatomy of tropical crop plants since a knowledge of their response to pathogens and pests depends on a knowledge of their normal structure. However, there are no detailed and comprehensive accounts of the structure of major tropical crop plants like coconut, oil-palm, coffee, cocoa, rubber, and so on. A particular deficiency is in studies of development morphology. The integrated activities of a diversity of workers is required here.

The conclusion then is that plant anatomy and morphology remains a central field of tropical inquiry, but not as an isolated or static discipline. The morphologist has to combine his specialized abilities with those of colleagues in other fields. Once this elementary principle is accepted we can move on to the more important task—devising the most efficient means to apply this principle.

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A CONTRIBUTION OF RAIN FOREST RESEARCH TO EVOLUTIONARY THEORY[1,2]

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Though by no means universal even in the lowlands, species diversity within a single life-form reaches unequalled levels in many tropical forests, and in particular in the aseasonal wet oceanic climates of the Far East. There large genera, many of whose species may occur together and are apparently spatially interchangeable (e.g., Poore, 1968) are particularly frequent and have prompted speculation as to their origin. Ecologists (Poore) and taxonomists (Fedorov, 1966; van Steenis, 1969) alike have concluded that chance events are the major determinants of survival and must hence influence the course of evolution. Janzen's (1970) attractive theory that interactions between host-specific predators and their tree prey provide a density controlling mechanism which allows accretion of floristic diversity has yet to be investigated within large tree genera and does not apply within the Dipterocarpaceae, dominant trees of the Far Eastern rain forest canopy, whose predators are well known and are not specific even at generic level.

How old are tropical tree species? How niche specific are they? Is evolution continuing within these forests? Are these communities in evolutionary equilibrium, following a long period of gradual stabilization (e.g., Stebbins 1974), or does species diversity continue to increase? What are the component tree species, are they outbreeders and are they genetically variable, or are they genetically uniform, even apomictic?

Richards (1963) has reasoned that ecology cannot afford to ignore the tropics; an understanding of the evolutionary biology of this most species-rich vegetation must be accepted as equally essential if only to put, by comparison, knowledge of our younger and less diversified temperate counterparts into truer perspective. Studies in the Dipterocarpaceae and their forests over the last 20 years, in which I have collaborated, are beginning to elucidate this subject.

The Age of West Malesian Forest Ecosystems

Haile et al. (1977) have established that the Malay Peninsula and southwest Borneo have remained within 20° N. latitude of the equator since the late Cre-

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[1] I have described the work of successful and happy collaboration in which I have been one of many participants: Paul Chai, Ilias Pa'ie, Othman Haron and Caroline Taylor in particular played a major part in the ecological research in Borneo. Engkik Soepadmo codirects the research on breeding systems which is being carried out by S. Appanah, Chan H. T., Gan Y. Y., Ha C. O., A. Kaur, and Yap S. K. under the supervision of J. I. Furtado, K. Jong, D. W. Lee, A. G. Marshall, J. D. Matthews, N. Prakash, F. W. Robertson and V. E. Sands at the Universities of Malaya and Aberdeen; this is supported by grants from the Leverhulme Trust Fund, the Royal Society of London, the U. K. Natural Environment Research Council and the Carnegie Trust for the Universities of Scotland.

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taceous. Muller (1968, 1972) has described the transition from gymnosperm forest to predominantly angiosperm forest during and following the Cenomanian, and the successive accretion of new orders and families through the Tertiary, from pollen analysis of the Plateau Sandstone formation of northwest Borneo. By the end of the Tertiary the inland forest flora was apparently not dissimilar to that of the present day, fossil leaves of putative Pliocene age from Manila for instance (Merrill, 1923) being identifiable with species still growing nearby. The pollen record suggests, on the one hand, that the region has remained within the humid, though not necessarily aseasonal, tropics since the origin of angiosperm forest, and, on the other, that the growth of floristic diversity at ordinal and familial level has occurred through a sequence of periodic and rather sudden immigrations, rather than through gradual evolution in situ.

The Quaternary era must inevitably have witnessed the invasion of seasonal rainfall regimes during the periods of eustatic fall in sea level, when the Sunda Shelf region, comprising the Malay Peninsula, Sumatra, Java, Borneo and the intervening seas, became a continent comparable in size and latitude to the northern part of South America; the last such time ended ca. 15,000 years B.P. The only evidence for climatic change in the lowlands during the Pleistocene is indirect, through the existence and gradual extinction of the nonforest large mammal and essentially Asiatic Trinil fauna during mid-Pleistocene times in Java (Medway, 1972). Evidence for the existence of periods of rainfall seasonality from other parts of lowland Sundaland during the Pleistocene is presently lacking. It is nevertheless difficult to believe that the extraordinary species richness of west Malesian forests, which is strongly restricted to the aseasonal region south of the Kangar-Pattani line in the Peninsula (Whitmore, 1975)—though generic diversity is not restricted to the same extent—has arisen in the last 15,000 years; the exceptionally high level of local endemism in some coastal regions, notably east and northwest Malaya and along the northwest coast of Borneo, almost certainly has a more ancient origin. Indeed, whereas localized centers of diversity and endemism exist in a sea of uniformity in South American forest ecosystems, and are considered to indicate the sites of refugia for rain forest species during the interpluvials, the greater part of the present west Malesian archipelago must be regarded as analogous to one vast refugium fragmented by the current high sea level.

Rate of Speciation Within West Malesian Trees

Muller (1964, 1972) has identified the pollen type of the monotypic riparian palm *Nypa* from as early as the Upper Cretaceous, and in another unique palynological study traced evolution within the mangrove genus *Sonneratia* and its fossil progenitor *Florschuetzia* since the Eocene. Plant distributions provide indirect evidence for continuing speciation during the Pleistocene and up to the present day; in this respect dipterocarps are particularly apt subjects owing to the absence of any known fruit vector. This may be exemplified by comparing distributional patterns in Dipterocarpaceae with the postulated Pleistocene geomorphological history of the northwest Borneo neogeosyncline (Ashton, 1972; Wall, 1967); the history of river capture neverthless remains to be confirmed by

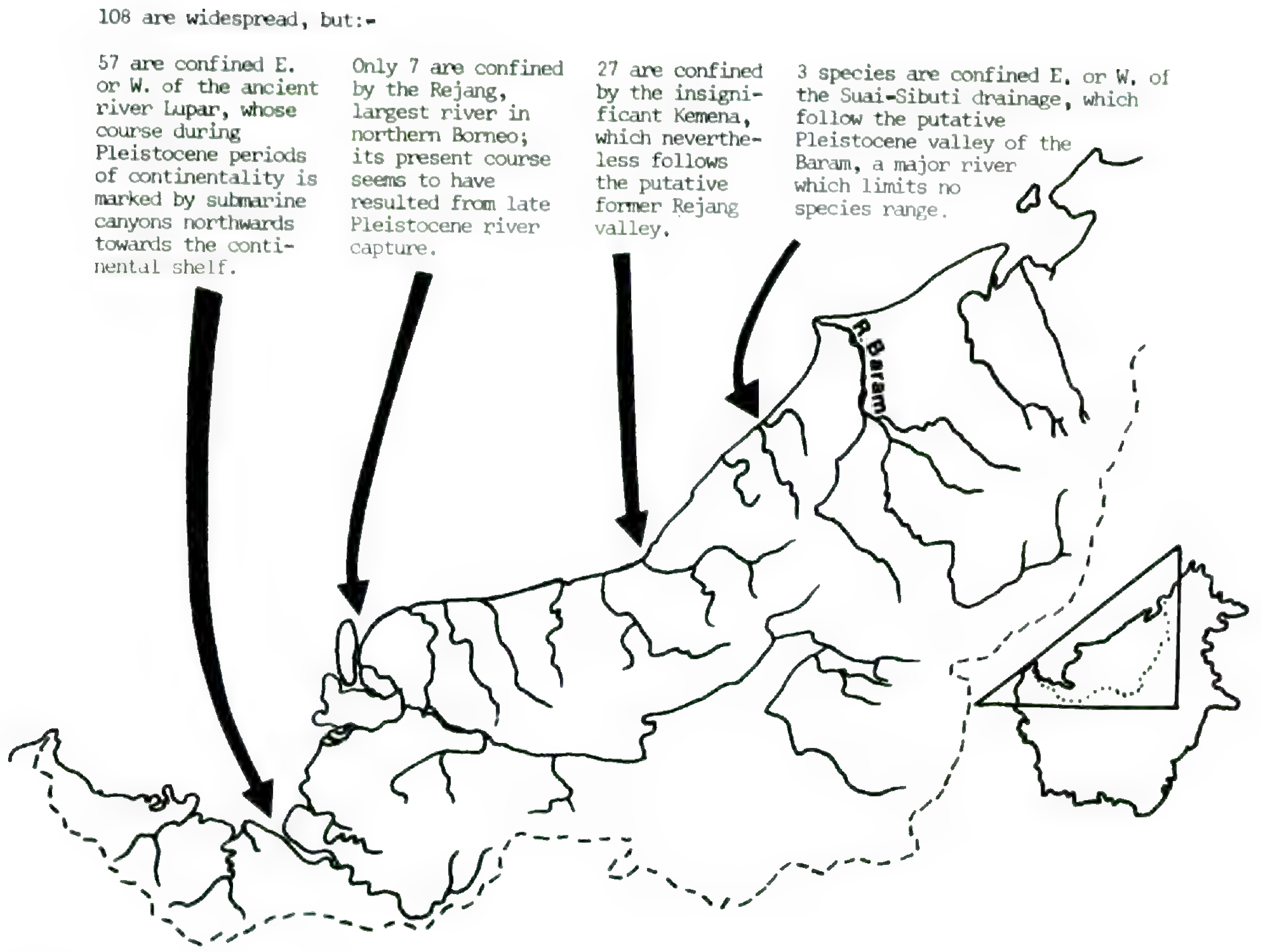

FIGURE 1. Geographical barriers and the distribution of 201 dipterocarps in northwest Borneo. The southeast to northwest trending drainage of northern Borneo is of probably late Pliocene-early Pleistocene origin.

analysis of river sediments. Though the major discontinuity in dipterocarp distributions follows a river valley of probably pre-Pleistocene origin, significant discontinuities also occur across valleys of lesser age, including examples of allopatric subspeciation (Figs. 1–2).

In some cases species may be remarkably recent in origin: The ten species of *Shorea* sect. *Pachycarpae* are endemic to Borneo, surprising in itself in view of its intermittent connection with the rest of Sundaland until the Holocene. Of these only one, *S. mecistopteryx* Ridl. is invariably morphologically clearly defined and at the same time widespread. The other widespread species, *S. pinanga* Scheff., *S. amplexicaulis* Ashton, *S. beccariana* Burck, and *S. macrophylla* (de Vr.) Ashton, are very variable and morphologically intermediate forms occur frequently in certain restricted localities. Of the remainder, at least two, *S. praestans* Ashton and *S. rotundifolia* Ashton, seem by their extremely local distribution, as well as by their morphological relationships with others, to be of very recent origin; the latter for instance occurs sympatrically, even side by side, with *S. amplexicaulis* with which it appears to be closely related.

Causes of Speciation: an Ecological viewpoint

Nevertheless, *S. rotundifolia* and the species in its section are exceptional among dipterocarps: Most species of the humid tropics are clearly defined;

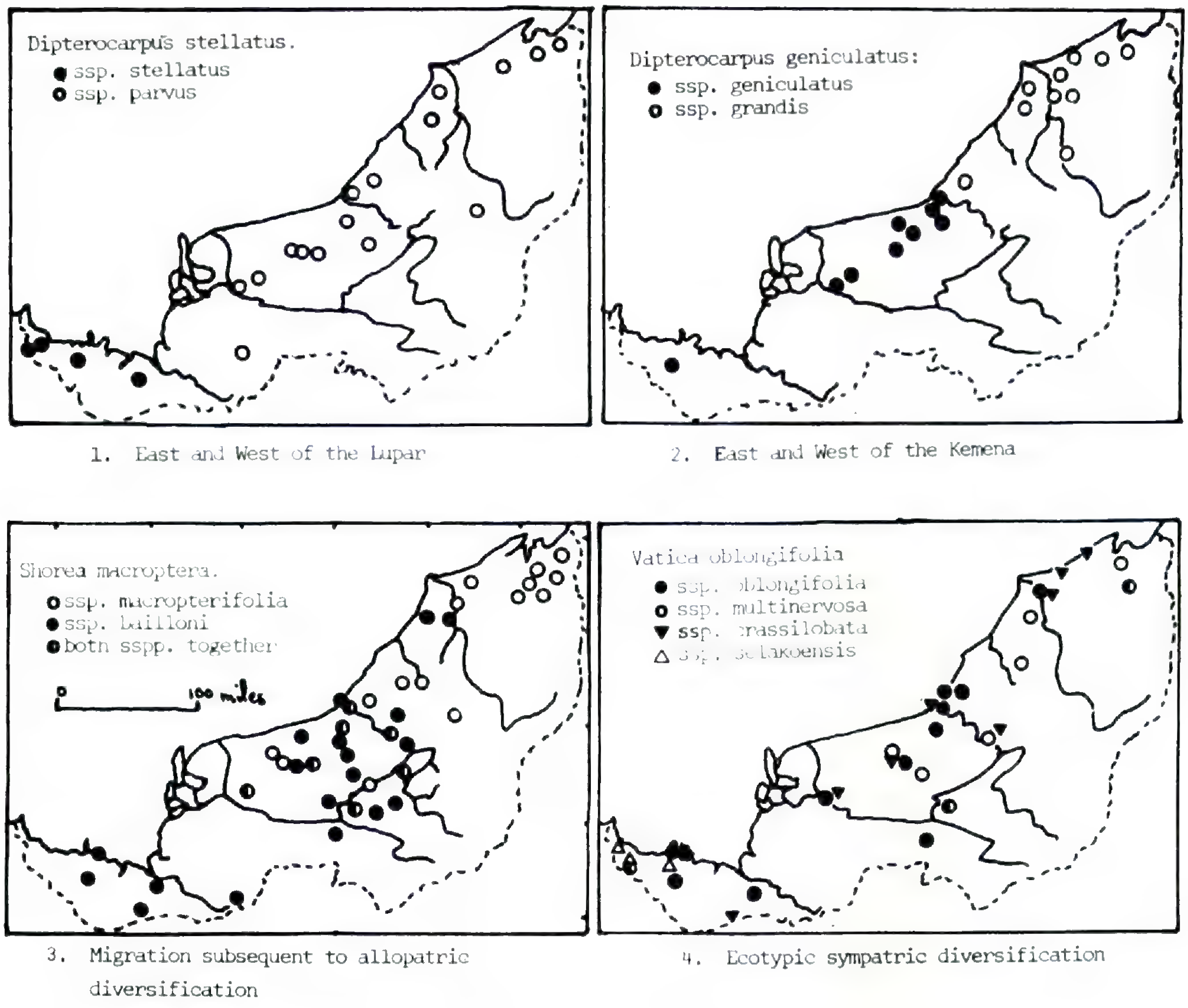

FIGURE 2. Patterns of speciation in dipterocarps in northwest Borneo.

closely related taxa are as a rule ecotypically differentiated in relation to site (Ashton, 1964, 1969), habit (Ashton, 1969), or physiology, as is the case with the commoner sympatric species of *Shorea* sect. *Muticae* (Symington, 1943). It is at the generic and familial level that taxa appear to be ecologically complementary, and it may be at this level that the importance of predator-prey interactions play a major part in the maintenance of diversity. This is yet to be studied, but it would be surprising if successful speciation occurred among rain forest trees in response to predators whose life cycle is likely to be at least one hundred times shorter.

Figure 3 shows that it is the extraordinary diversity at species level which distinguishes Malesian forests from all others. The sample from mixed forests in Surinam (calculated from Schulz, 1960, and probably a slight underestimate as species in some genera were not all distinguished) produced the same genus to species ratio as that from the isolated relict forests of southwest Sri Lanka, notwithstanding the higher number of genera in the former, a reflection of its continental location. Pasoh forest has one of the lowest ratios calculated for Malesian Mixed Dipterocarp forest (e.g., see Ashton, 1976a).

Mixed Dipterocarp forest differs considerably between sites, both in species

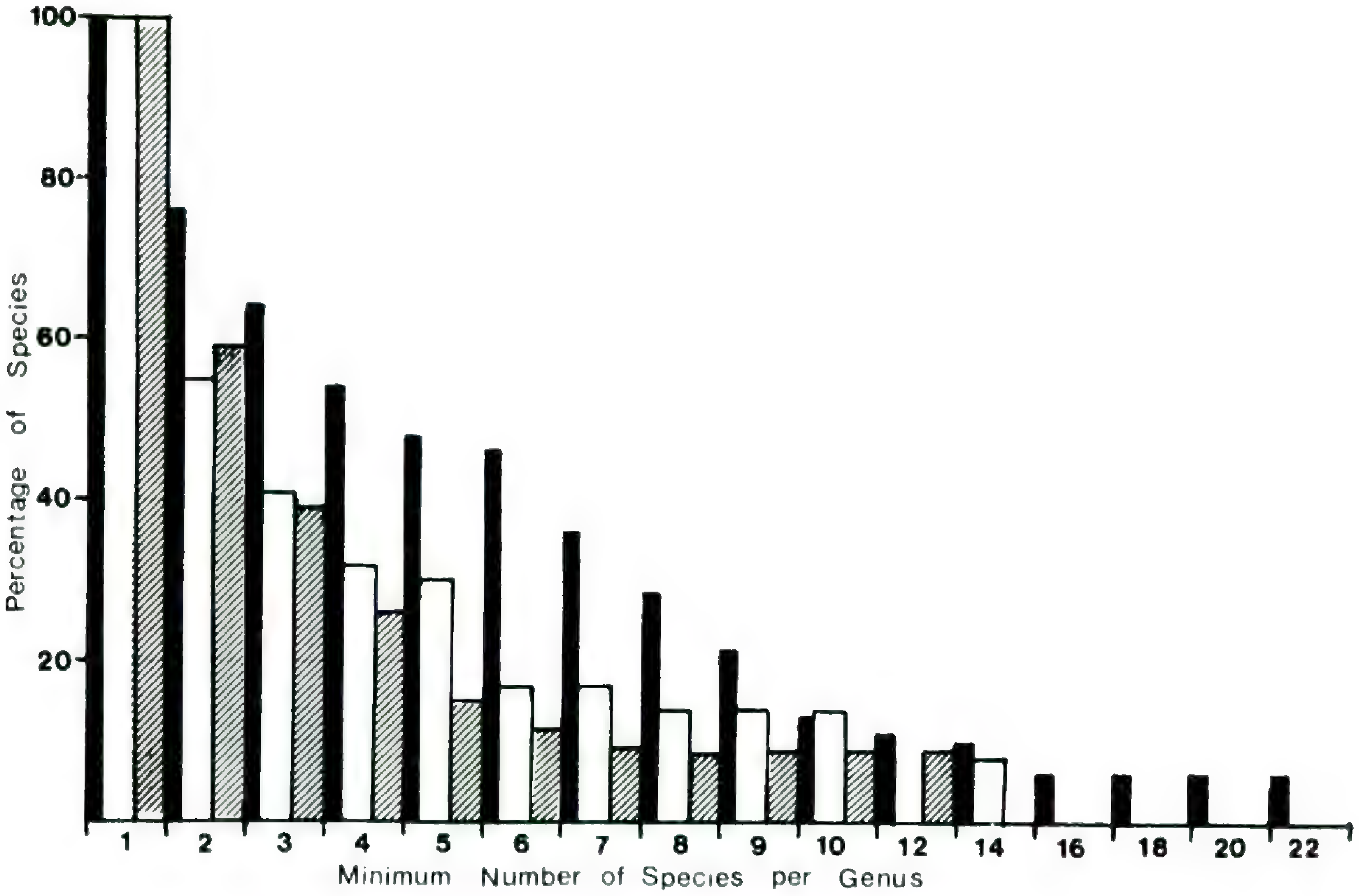

FIGURE 3. The percentage of species in genera of different sizes in samples of uniform mixed lowland rain forest. Solid columns: Pasoh Forest, Malaysia (2 × 5 ha; 191 genera; 484 species; ratio 1:2.5). Empty columns: Sri Lanka (3 × 2.5 ha; 98 genera; 166 species; ratio 1:1.7). Hatched columns: Mapane, Surinam (5.6 ha; 152 genera; 255 species; ratio 1:1.7).

richness and in degree of floristic spatial variability; and both seem to be influenced by soil nutrient status. Our work in northwest Borneo indicates that spatial variation is measurably correlated with soil nutrients only where fertility is low; total phosphorus and exchangeable potassium become increasingly correlated when phosphorus levels are below ca. 200 p.p.m. (Fig. 4; Ashton & Brunig, 1975; Ashton, in preparation). Intrinsic floristic richness appears to be greatest where exchangeable potassium is between 1,000–2,500 p.p.m. (Fig. 5). Here a species/individual curve for a Heath forest site is compared with six others, selected to exemplify a general trend among 18 sites in Malaysian Mixed Dipterocarp forest where I have carried out quantitative studies. The Pasoh curve is representative of the Mixed Dipterocarp forest of the Malay Peninsula, noted for its floristic uniformity (Wong & Whitmore, 1970, though see also Ashton, 1976c), growing in a region of Lower Palaeozoic rocks that are the oldest in west Malesia, and on an ancient land surface that has remained above sea at least since the Cretaceous. The plot was sited on Pleistocene raised riverain alluvium to ensure uniformity; forest on adjacent hillside in the event produced a very similar species/area curve. The Arip and Mersing sites each represent small islands, in neither case exceeding 50 km^2, of an unusual substrate in the sedimentary rocks of the geologically and geomorphologically young Neogene basin of northwest Borneo; the former in fact consists merely of a narrow ridge, rarely exceeding 1.6 km wide. Bukit Lambir, near the youngest part of that basin, is Upper Miocene sandstone. These curves suggest then that intrinsic floristic di-

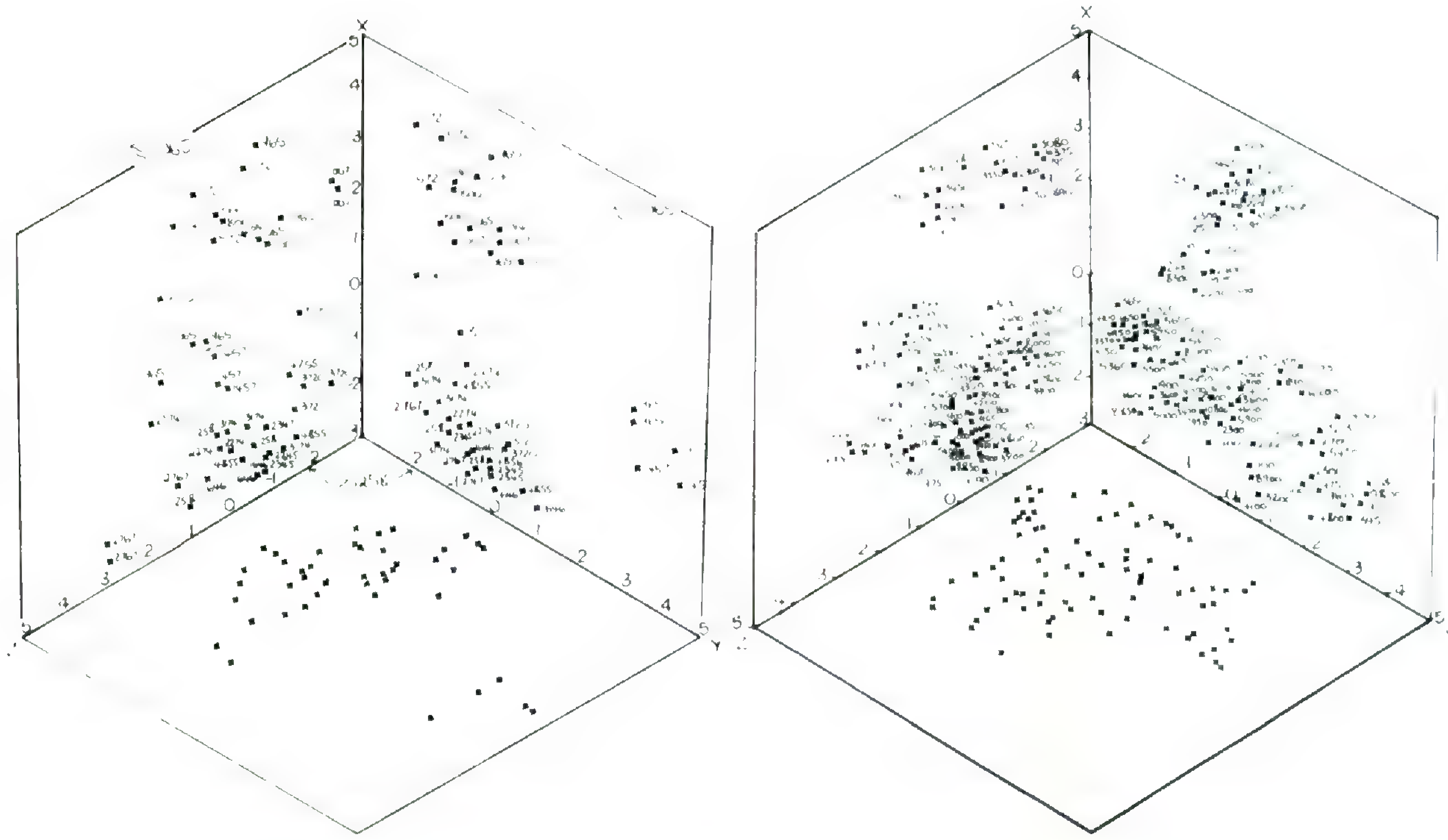

FIGURE 4. Principal components ordinations of 0.2 ha plots in Mixed Dipterocarp forest: Values for exchangeable K (in p.p.m.) are superimposed. Left: Bukit Iju, Arip (rhyolite). Right: Bukit Mersing, Arap (basalt).

versity within this region of probable Pleistocene climatic continuity is a function neither of geological or geomorphological age, nor of the area of uniform terrain and its potential influence on diversification and extinction. They do suggest that an equilibrium may be reached, in which either no further speciation is occurring, or immigration and speciation are being balanced by extinction; and that in the absence of disturbance the level of this equilibrium is determined by soil conditions.

Genetic Variation in Species Populations and its Maintenance

It is as a consequence of these discoveries that a group of collaborators in the University of Malaya and the University of Aberdeen, including both staff and research students, has been investigating the genetic variability of tree populations in the mature phase of primary rain forest in Malaya, and the underlying characteristics of cytology, embryology, and reproductive biology, including the behavioral ecology of pollen and fruit vectors, associated with it. This research, centered at the Pasoh Forest, is presently in progress and mention will therefore only be made to results already submitted for publication.

The two principal species under study are *Shorea* (sect. *Muticae*) *leprosula* Miq., a common, widespread and morphologically well defined and rather uniform emergent dipterocarp, and *Xerospermum intermedium* Radlk., Sapindaceae, an understory fruit tree with similar distribution and variability. Electrophoretic analysis of isozymal variation of populations of both species, coupled with biometric analysis of morphological variation by Y. Y. Gan (Gan et al., 1977) suggest that both have high levels of genetic polymorphism, but that vari-

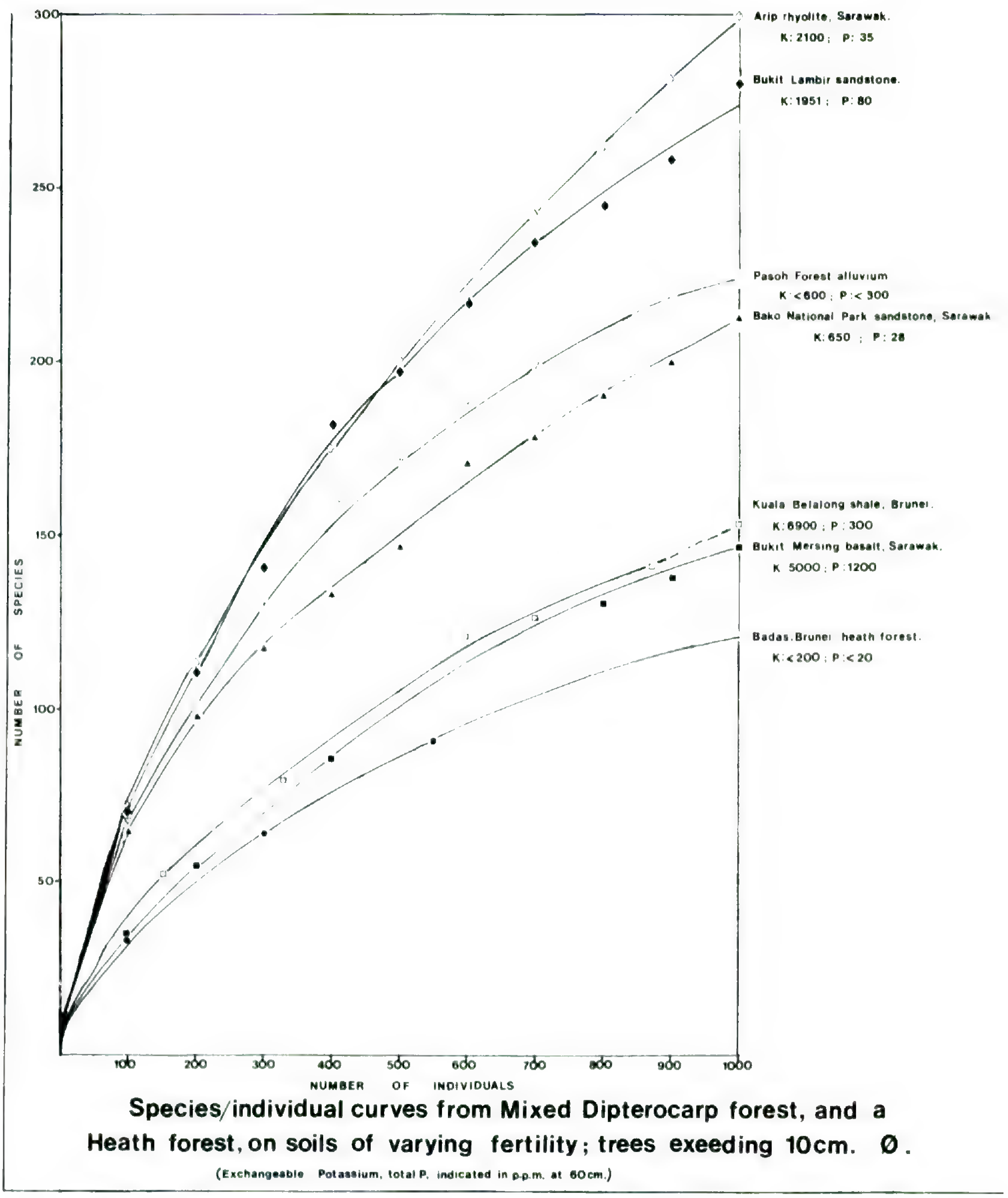

FIGURE 5. Species/individual curves from Mixed Dipterocarp forests and a Heath forest.

ation in gene frequency is short range. It is inferred from this that they are outbreeders with restricted pollen and fruit dispersal; this is being confirmed by studies of pollen compatibility and reproductive and vector biology (S. K. Yap, H. T. Chan & S. Appanah, in preparation). A. Kaur and C. O. Ha (Kaur et al., 1978) find both species to be diploid, with normal embryogenesis of the *Polygonum* type. Chan has also confirmed high levels of self-incompatibility in two species of *Shorea* sect. *Pachycarpae* and successfully secured fruit formation from an artificial hybridization between them.

These species therefore conform to the pattern expected of long-lived plants in stable environments (e.g., Stebbins, 1958) and to the prevailing trends observed by Bawa (1974, 1975, 1977) in similar studies in Costa Rica.

Nevertheless, *Shorea leprosula* and *Xerospermum intermedium* were chosen for study for practical reasons, owing to their relatively high population densities at Pasoh: 5 per ha exceeding 10 cm diameter for the former, 10 per ha for the latter, the mean for all species being 1 per ha. Species with low population densities comprise the vast majority, and it might be expected that maintenance of free gene exchange may be more difficult among them. Gan et al. (1977) found a very low level of genetic polymorphism by isozyme analysis in *Shorea ovalis* (Korth.) Bl. ssp. *sericea* (Dyer) Ashton, a result which may nevertheless be an artifact caused by the fact that this species is a tetraploid (Jong & Lethbridge, 1967). Jong (1976) reported meiotic irregularities in the same species. Chan (in Gan et al., 1977; Kaur et al., 1978) found that *S. ovalis* appears to be fully self-compatible, and, though lacking the close intraspecific flowering synchrony that is a characteristic of most dipterocarps, it has a more uniform than average fruiting success rate. A. Kaur (Kaur et al., 1978) has now confirmed that apomixis occurs in this species and at least one other through adventive polyembryony. Apomixis is also inferred through the constant occurrence of triploidy in root squashes from several seedlings originating from a single tree, and from the production of more seedlings from a fruit than there are ovules in several others. Among 16 dipterocarp species studied quantitatively by us, 10 at least sometimes produced multiple seedlings from the normally 1-seeded fruit, though this does not confirm polyembryony as the dipterocarp ovary initially bears 6 ovules. In the four species in which several individuals were under observation the proportion of seeds producing multiple seedlings varied widely between individuals. Though it is unlikely that apomixis occurs through adventive polyembryony in all species producing multiple seedlings, it equally cannot be assumed that it does not occur in species in which only single embryos develop.

C. O. Ha (in Kaur et al., 1978) has inferred apomixis in the dioecious understory tree *Garcinia parvifolia* Miq., and has inferential evidence for its occurrence in other species of *Garcinia*. If we accept Grant's (1958) view that dioecism is itself a derived condition, then apomixis must here be regarded as evidence of extreme derivation, and an example of the advanced evolutionary levels that can occur, presumably as a result of natural selection, in the rain forest environment.

Though it can hardly be claimed that these few species can adequately represent the West Malesian lowland tree flora as a whole, they do conclusively demonstrate that apomixis occurs within those series of closely allied species, occurring together in the same habitat, which are such a unique character of that region.

An unexpected observation is that those species whose genecology might be expected to favor allopatric diversification and distinct discontinuities in variation, *Shorea leprosula* and *Xerospermum intermedium*, are remarkably uniform throughout their wide range, while every one of the dipterocarp taxa in which

apomixis is inferred or confirmed are morphologically distinct and possess closely allopatric distribution patterns. Some, such as *Shorea ovalis*, occur in relatively high density populations and are widespread, while others such as *Hopea subalata* Sym. are extremely local; this will form the subject of a forthcoming paper.

TOWARDS A SYNTHESIS

To help identify priorities for future work we suggest the following hypothesis to explain our observations: In the uniform physical environment and predictable climate of lowland Malaya natural selection will be dominated by biotic factors. These factors will continuously change in time through the periodic accretion of immigrant species into the forest community, each newcomer thus inevitably modifying the competitive interactions of those already present. The maintenance of genetic variability within species is therefore essential to their long-term survival, and maintenance of cross-pollination is at a premium. As the density of the forest community as a whole cannot increase, it must follow that the arrival of new species, and particularly those which successfully build up relatively high population densities must lead to a compensatory decline in the population density of those already present. This will hasten the decline of species whose densities are already low by increasing the physical difficulty of cross-pollination from increasingly distant pollen sources as Fedorov predicted; this in turn will lower fruit yield and weaken the reproductive pressure required for maintenance of numbers. Natural selection in species with very low population densities—and these could constitute the majority—might well favor genotypes that are both well adapted and can maintain reliable and high fruit production. It is suggested therefore that apomixis has originated in rain forest trees once again as a means of overcoming sterility, as suggested long ago by Darlington (1939).

We might infer, from the variability between trees in the proportion of multiple seedlings produced, that apomixis occurs in only a proportion of trees in some species populations. It is difficult nevertheless to see how a balance between the number of apomictic and/or self-compatible, and obligate outcrossing individuals can be maintained in perpetuity, for increasing rarity due to changing interspecific competition would lead to increasing decline in the proportion of obligate outcrossing individuals. Conversely obligate apomixis, or gene fixation in small isolated populations of self-compatible individuals, must itself be regarded as an evolutionary dead end, preluding inevitable extinction in a continuously changing biotic environment. Thus the maintenance of low levels of self-compatibility, and sufficiently high population densities to ensure adequate reproductive pressure to maintain numbers through outcrossing are both essential adjuncts to long-term survival of a species. If obligate apomixis does frequently occur (and this requires much more study) and if our hypothesis is correct, we may see in the ancient Malayan rain forest a phenomenon which must eventually arise in all plant communities: there must be an ultimate limit to the level of intrinsic species diversity that can be attained, beyond which accretion is balanced by extinction (see also discussion in Whitmore, 1975).

We have here an analogue of G. G. Simpson's (1953) "evolutionary episode"

in the context of a multispecies community. Invading species, we suggest, are mainly outbreeders, but the low densities of even the commonest species combine with limited pollen and fruit dispersal to favor rapid allopatric speciation; such species will prevail in young forest communities and this can be tested in the isolated forests of volcanic islands or the Atlantic foothills of the Central American Cordillera. When numbers decline through competition, and as the overall floristic diversity increases, selection will increasingly favor apomixis which may then be an agent of secondary, essentially ephemeral and possibly sympatric, speciation. Thus the declining species do not fade away gradually but, by borrowing time in a Faustian pact of apomixis, regain the stage from time to time before their inevitable nemesis.

Conclusions

We now have growing evidence then that Malesian trees of the mature phase of primary rain forest are highly niche specific; that some may be old, but that speciation is actively continuing among many others; that there is a maximum number of species that a forest can accommodate, that this varies with site conditions and that it has already been approached in west Malesian forests; and that a remarkable variety of breeding systems exists even within the mature phase alone. An overall picture is thus beginning to emerge in which each part of the puzzle is becoming interlocked, but it hardly confirms Stebbins's (1974) picture of the tropical rain forest as merely a repository for botanical antiques!

But what of the gap phase species—the woody pioneers? How have so many archaic forms continued to survive nevertheless? And what are the mechanisms that allow species diversity to reach its highest level on relatively infertile soils? A student of ours is about to embark on a study of the first, and we are planning to pursue the others in the near future. But our forest of ignorance is deep and vast, and for all its intriguing mystery attracts far too few explorers.

Once again the fascination of academic theory has dominated my presentation, but what are the realities on the ground? Raven (1976) has eloquently described the demise of this unique vegetation; man's destruction in pursuit of short-term gains will lead to long-term disaster for humanity, as inevitably as apomixis may for my proud dipterocarps. Everywhere it is the same—uncontrolled and injudicious logging practices and immigration of peoples unfamiliar with local agricultural conditions, leading to destruction of the hydrological balance of catchments, physical erosion, flooding and silting of the fertile plains, the supremacy of perennial herbaceous weeds, and the final destruction of social systems and starvation. We biologists have for too long pointed our accusing fingers elsewhere, at the politicians, financiers, even the poor peasants, anyone but ourselves. I would suggest that two of the most intractable problems are essentially scientific: The lack of critical research into the most effective means of bringing about progressive change in land use based *both* on scientific innovation and traditional practices and values; and the tendency for us scientists to go for the easy options—be it the investigation of an isolated academic problem or the development of a technique to enhance short-term profitability without regard to its wider implications—and to fear the interdisciplinary collaboration

on a broad front that alone can provide the prescriptions needed. Our little venture may claim to be a hesitant start in the right direction (Jong et al., 1973; Ashton 1976a, 1976b), for in it we combine research education with a conscious choice of species which have potential in plantations, for timber and fruit. Now we must use the knowledge we have gained to experiment in the establishment and improvement of new crops for new lands—those that were considered unexploitable by traditional farmers and are now all that is left. We must get these crops from the much-heralded gene pool of the forest, and this we plan too. But we will need economists, agronomists, social anthropologists, and others besides before our work can reach the stage of practical applicability. Above all, we need collaboration.

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PROMISING DIRECTIONS OF STUDY IN TROPICAL ANIMAL-PLANT INTERACTIONS[1]

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Plants are not just food for animals, and animals are not just decorations on the vegetation. The world is not green. It is colored lectin, tannin, cyanide, caffeine, aflatoxin, and canavanine. And there is a lot of cellulose thrown in to make the mix even more inedible. Animals are not ambulatory bomb calorimeters. They starve, they ache, they abort, they vomit, they remember, they die, and they evolve. Peter Raven asked me to write about promising directions in tropical animal-plant interaction studies, mostly because he believes there are some. Well, it's roughly analogous to standing in the city of London after WWII and saying, well, let's get on with studying the promising directions in London's architectural history.

My paper is about tropical interactions; they are the first to be extinguished by man's onslaught and the last to be lamented. Interactions have several traits that make them especially inconspicuous (Janzen 1974a). (a). The participants, being to some degree self-sufficient, may persist well after the interaction that produced them is gone; a *Scheelea rostrata* palm left standing in a Costa Rican pasture will persist long after the agouti that buried its seed and the forest that gave dry season shade to its seedlings has been removed (Janzen 1971a). (b). Humans eat participants, not interactions; being relatively incompetent until quite recently, humans have by and large not generated cultural rules for the maintenance of interactions per se, but rather for the preservation of the participants. (c). Humans eat only certain participants, and often atypical ones; if the interaction is to be preserved, it is not the overall interaction in which the participant happens to be imbedded that is preserved, but rather that subinteraction which will generate the largest number of participants for dinner. (d). The systematics and taxonomy of interactions is hopeless; most of the types have already been mutilated or destroyed and what is perhaps even worse, it is virtually impossible to look at an interaction and know if it is largely intact. (e). You cannot collect an interaction and keep a specimen on display in a museum. (f). An interaction has no material potential worth, as opposed to the participants which can be noticed and retained if for no other reason than the optimistic view that some day a use may be found for one of them. However, and this is a big however, I must add in the same breath that it is as examples of how things can happen that interactions are the most valuable and therefore most deserving of preservation. The big problem is that human wants are generally so unrepresentative of organisms in general; the specific interactions desired by humans are not

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likely to be found in nature but rather will have to be hand-tailored with the desired participants.

Now after that pessimistic preamble, I am still left with the task of pointing at some promising directions in the study of tropical animal-plant interactions. There are many. I take them in no particular order, and if I ignore one of particular importance to you, view it as oversight and not an evaluation. Rather than preach that we should study this or that, I will simply give brief examples to draw attention to mysterious patterns, curious new hypotheses, and perplexing observations. Gilbert (1977) has, on the other hand, presented somewhat of a challenge when he stated that "It is not clear, however, that further base-level exploration would provide many new ecological or evolutionary insights, or that additional categories of interactions would be found which fall outside those major kinds that have so far been described." I wonder.

Any person seriously interested in tropical animal-plant interactions should take a week or two to read the recent symposium and review publications in this area (Van Emden, 1973; Luckner et al., 1976; Burley & Styles, 1976; Gilbert & Raven, 1975; Wallace & Mansell, 1976; Jermy, 1976; Levin, 1976; Gilbert, 1977) and browse the numerous papers on this subject in the post-1969 issues of *Ecology, American Naturalist, Science, Biotropica, Oecologia, Journal of Animal Ecology, Journal of Applied Ecology, Evolution*, and the *Annual Review of Ecology and Systematics* (among others).

Plant Productivity and the Animals in the Habitat

At the lowland Pasoh rain forest, Negri Sembilan, Peninsular Malaysia, I censused the plants in flower that were less than 3 m tall in the understory of undisturbed forest along 3 km of narrow trail (early September, 1976). I found one orchid, one 1.5 m tall Araliaceae, one 0.5 m tall Acanthaceae (*Lepidagathis longifolia*), and one 1 m tall *Ixora*-like Rubiaceae. In the lowlands of the national park, Taman Negara, 5.4 km of rain forest trail yielded one white-flowered ginger, two *Ixora*-like Rubiaceae, one Acanthaceae, one unknown family, and two 10–20 cm tall Gesneriaceae with underground stems. In primary forest understory in the new Corcovado National Park (20–160 m elevation, Osa Peninsula, southwestern Costa Rica), a trail-side survey of 4.3 km yielded 94 plants in flower of 18 species (20 November 1976). In other words, I averaged 1.3 plants in flower per kilometer in the Malayan rain forest understory and 21.9 plants in flower per kilometer of Costa Rican rain forest understory.

These woefully small samples reflect accurately my general impression of the general abundance of flowers in the understory of rain forests of Peninsular Malaysia and Sarawak, as compared with those of Costa Rican rain forest of similar elevation. I was informed locally that 1976 was one of the heaviest years in memory for flower and fruit production in Peninsular Malaysia; November is the time of most reduced flower production in Costa Rican rain forest understory (and see Frankie et al., 1974). In short, if one were to turn loose in Pasoh or Taman Negara the rain forest understory fauna of flower-visiting hummingbirds, butterflies, moths, and bees found in the Corcovado, I predict that they would be dead of starvation in a few days. Furthermore, they could not survive

by moving out into secondary regeneration; Malaysian disturbed sites have a grossly lower flower abundance than any weedy wet-season vegetation that I have seen anywhere in the African or neotropical lowlands.

Over the Malaysian transects mentioned above, I encountered 63 understory individuals in fruit (22 species) for an average of 7.5 per kilometer. In the Corcovado forest, there were 345 individuals in fruit (34 species) for an average of 78.4 per kilometer. Again, the fauna of understory birds that frequently eats small fruits in neotropical rain forests would have a very rough go of it in the Malaysian forests.

It is extremely interesting that after doing this and writing the above, I discovered Karr's (1976) statement that "about 80% of the canopy and understory tree species on Barro Colorado Island are dispersed by animals (Foster, 1973), while only about 10% of the trees on Fogden's (1972) [Sarawak] study area were important as sources of fruits for birds." Furthermore, at the IV International Congress of Ecology in Panama, Karr (March, 1977) noted that "The most striking difference is the total lack of undergrowth frugivores in mist-net samples taken from Malaysia as compared with 25–33% of the individuals captured in undergrowth of African and Central American forest."

I would like to propose a rather sweeping hypothesis to account for this paucity of flowers and fruits on rain forest understory shrubs, a paucity which should have a very depressing effect on the biomass and species richness of the understory fauna. I need first, however, to belabor you with three facts about the lowland Malaysian rain forests in which the censuses were made.

(a). They are dipterocarp forests, which means that between 50 and 80% of the tree crowns in the canopy belong to species of Dipterocarpaceae. The members of this family, in Malaysia and some other tropical Asian areas, mast fruit within (and between) habitats. Thus the bulk of the flower and fruit production by better than half of the upper canopy photosynthetic machinery is pulsed at 3 to 11 year intervals. Associated with this, the animal community is sufficiently satiated by the enormous numbers of seeds that a very large number survive to the seedling and small sapling stage (Janzen, 1974b).

(b). Malaysian rain forests, on the Malay Peninsula or in Sarawak, are largely perched on sandy soils ranging from very old white sand deposits (such as in Bako National Park, Sarawak) to very sandy soils derived from weathering of granitic base rock that has not been inundated by the sea for an extremely long time. There is no volcanic overlay nor crust of weathering limestone on the majority of the terrain. There are many indirect measures of the relatively low ability of these soils to generate a vegetation with a high harvestable productivity for other organisms: when cleared, the second-growth vegetation is very slow to refill the site (Janzen, 1974b, 1974c, and this is probably why plantation rubber is so successful on these soil types); the forest has largely remained uncut and unexploited by agrarian peoples despite their presence in the general area for many thousands of years (note that virtually all of nearby Java on volcanic soils is under agriculture); second-growth vegetation of the sites has an amazingly low insect biomass as compared to that of comparable neotropical weedy sites (Janzen, 1974b); etc.

(c). There *are* bees, butterflies, flower-visiting birds, small fruit-eating birds, etc. present in the Malaysian rain forests. In other words, pollinators and dispersal agents can be drawn from these groups if the ecological and evolutionary opportunity is presented.

I hypothesize that the shortage of rain forest understory flowers and fruits is largely attributable to two forces operating simultaneously and synergistically. First, I hypothesize that the large pulse of dipterocarp seedlings and saplings takes up a large part of the resources that are available to neotropical understory shrubs; the dipterocarp offspring are apparently dying in large part through competition rather than through supporting a seed-predator guild. Simultaneously, they are analogous to an enormous and very generalist herbivore in their impact on understory shrubs. Since dipterocarp seedlings never flower or fruit, they take a large portion of the understory resources without feeding part of it back into the flower-visitor and fruit-eater guild so conspicuous in a neotropical forest. Second, I hypothesize that as the soil conditions get progressively worse, the ability to be a reproducing individual in the light-poor understory is reduced. That is to say, irrespective of the presence of the dipterocarp seedlings, if the forest canopy is held constant and the soil fertility is depressed, the biomass (number of individuals in general) and reproductive output per ha by understory shrubs should fall (just as it would if soil fertility were held constant and the light were decreased). In other words, the rain forests of Malaysia sit on a poorer piece of real estate than do those of lowland Costa Rica, and the flower and fruit density in the understory reflects this.

The animals are probably woven into this matrix more firmly than I have indicated so far. I have hypothesized that the habitat-wide masting behavior of these Dipterocarpaceae is driven at present, and was selected for in the past, by the seed predators in general (Janzen, 1974b). Further, I have argued that the lower the overall productivity of the site, the more likely it is that the animals will select for masting behavior because the less food there is for them between mast crops, the more severely they are depressed in density by masting behavior. But the scarcer they are between mast crops, the fewer understory flower and fruit crops they can (will) visit; the fewer crops they visit, the less well off will be such plants and the better off will be the dipterocarp seedlings in competition with nondipterocarps. Why doesn't the system progress to where there are nothing but seedlings and saplings of overstory trees in the understory? Probably because as time passes since the last mast crop, competitive and accidental deaths clear the arena for some other species of plants, and because a number of animals that visit flowers in the understory can also go elsewhere for food; many frugivores can feed on insects and other food types when understory fruits are scarce.

The focus to this point has been largely on the biomass of flowers and fruits, and associated animals. However, the species richness of plants and animals should also be negatively influenced by a reduction in harvestable productivity (Janzen, 1977c). My argument involves resource partitioning and specialization on the partitions. In short, as the productivity of harvestable resources in the habitat falls, more and more resource blocks become too small to sustain a spe-

cialist. They are then taken by a more generalized harvester or by another trophic level. In the context of the example under discussion, the number of flower-visiting species of understory birds should decline as the soil gets poorer and as the overstory becomes progressively more synchronized at supra-annual seeding. For example, in a Costa Rican rain forest there are species and morphs (often females) of hummingbirds (e.g., *Phaethornis* spp.) that specialize on widely scattered understory individuals in flower, and species and morphs (often males) that specialize on large clumps of flowers on forest edges (e.g., Stiles, 1975). From what I have seen of Malaysian lowland rain forest, a hummingbird would have to forage at all such sites and then some to stay in the game. Simultaneously the species richness of seed predators in the habitat should also decline as soils become poorer and synchrony increases, since the progressively more pulsed nature of the seed resource makes it effectively scarcer in any but the very exceptional mast year. For example, in a Costa Rican rain forest there is a large standing crop of agoutis (*Dasyprocta punctata*) and pacas (*Cuniculus paca*) that live on the rather continuous input of fruits, seeds and young seedlings (e.g., Smythe, 1970). These animals are relatively sedentary. They do not have ecological analogues in Malaysian forests, and I suspect the reason to be that in most years the seed resource is not large enough to sustain them, though in mast years it is far greater than they could ever consume before the seeds germinate.

The pulsing of productivity in a rain forest can have other interesting side effects on animals. It should select for migratory or very nomadic species, which are in turn less likely to develop local regional populations than are more sedentary species. I have argued that the wind-dispersed nature of dipterocarp seed (and that of other trees that fruit as they do, such as the legume *Koompasia*) is due to their specialization to the site on which their parent grew and is not involved in escape from seed predators through dispersal (Janzen, 1977d); it may also be due to an extreme shortage of biomass of frugivorous animals owing to the fact that much of the seed production by the forest is pulsed (the frugivores would be severely satiated on seeding years, just as would be the seed predators). Whatever the cause, the fact that most of the canopy-level seed production is wind-dispersed eliminates a large portion of the fruit input that is an important part of the diet of many neotropical animals. For example, I doubt very much that any Malaysian forest comes anywhere close to the figures of 1.93 g of fruit per m^2 calculated to fall in a Panamanian rain forest by Smythe (1970). However, in closing this paragraph, I cannot help but notice that Malaysian forests have an exceptionally high number of species of squirrels (e.g., 19 tree squirrels in Borneo; Davis, 1962). It is possible that squirrels are particularly good at dealing with a highly pulsed food input, as compared with the other animals that eat seeds and fruits (some in fact, are specialists on insects or vegetative parts of plants). In short, as harvestable productivity becomes progressively less available, there is no reason to expect all animal life forms to be depressed at the same rate. In fact, the elimination of some could quite reasonably result in an increase in others.

The ramifications of low productivity of harvestable resources by the plant

community in an average year can produce a multitude of higher-order interactions. For example, in 17 days of fieldwork and travel between field sites by boat or small car, I saw a total of three raptorial birds in Peninsular Malaysia (and none in 11 days in Bako National Park, Sarawak). The area traversed was at least 480 km of urban, rural, and forest roads, 122 km of large river through farmland and forest reserve (Tembeling River on the way to and from Taman Negara), and about 50 hours of hiking in forest reserves. At least 80% of the weather was nonrainy. I should emphasize that I was not searching for raptorial birds, but rather just watching for any kind of animal. In a similar excursion up and down the similar-sized Sanaga River in Cameroun, I took photographs of 23 birds of prey and saw at least 50 more. In Ugandan and Kenyan forest-farmland and national parks, it is hard to find a moment on a clear day when a raptor or large avian scavenger is not in view somewhere (and see Janzen, 1976a). In Costa Rican lowland rain forests, forest-farmland mixes, and open pasturelands, raptors and/or scavengers are seen at least once every several hours, and much more often in many circumstances.

The ornithological literature is not designed so as to provide material relevant to comments such as those above. However, a few interesting tidbits can be extracted. For example, the black or king vulture (*Torgos calvus*) is common throughout the northern part of the Malay Peninsula but is almost never seen in the southern half (rainforested portion) of the peninsula; the same may be said of the other peninsular vulture (*Pseudogyps bengalensis*) (Robinson, 1927; Medway & Wells, 1976). As Wells put it (personal communication), there is no vulture (for all practical purposes) in West Malaysia. The standard explanation for the absence of vultures is Robinson's (1927) comment that "securing their food entirely by sight, it is obvious that a heavily forested country is quite unsuited to them and it is for this reason, probably, that they do not extend to the Malay Archipelago." This seems to me to be a quite inadequate explanation. As Peninsular Malaysia has been cleared, vultures have become rarer, not more common (Robinson, 1927). Furthermore, one has to ask (1) why similarly heavily forested areas in other parts of the tropics sustain vultures, (2) why the forest was not cleared for agriculture and livestock long ago as it was in other parts of the tropics, and (3) why the contemporary invasion of agricultural peoples does not bring with it adequate food for vultures? In short, I hypothesize that rain forest Peninsular Malaysian and Sarawak habitats never did generate enough carrion to keep vultures in the game, and that the contemporary peoples occupying these habitats cannot raise enough livestock to generate enough spin-off carcasses for vultures to persist as the land is cleared. Central American rain forest and associated natural disturbance sites, when put into multi-use agriculture and livestock husbandry, sustain conspicuous populations of three species of vultures and two caracaras (hawks that act like vultures).

I doubt that the paucity of vultures or vulturelike birds in Malaysia is due to excessive hunting; however, if there is less food for them, then even small amounts of hunting can do disproportionately more damage than if there is a large resource base. I doubt that the large varanid lizards, relatively common on riverbanks and in refuse dumps where not hunted, are competitively exclud-

ing the vulturelike birds. I saw 28 large (0.5–1 m snout–vent) *Varanus* along the bank of about 20 km of the Tembeling River at and below Taman Negara on one morning. Rather, I suspect that the absence of vultures allows the presence of these relatively slow scavengers; if the food is scarce and occurs at very long intervals, then a cold-blooded professional starver would be able to maintain a much higher biomass than birds. I was told by a Kuala Lumpur "pet" dealer that with water, a large varanid can live a year without food; I doubt a vulture could do the same.

The hypothesis that the natural habitats of West Malaysia generate a low density of food for large carnivorous birds is also supported by the species richness of falconids and accipiters. West Malaysia has 11 resident species of accipiters and 1 resident falcon (Medway & Wells, 1976) and is about 132,000 km^2 in area; Costa Rica has at least 28 resident species of accipiters and 8 resident falcons and is 51,000 km^2 in area (Slud, 1964). The tiny Costa Rican rain forest field station at Finca La Selva (6.1 km^2) has at least 9 resident accipiters and 4 resident falcons (Slud, 1960).

Herons, bitterns, and egrets are conspicuously scarce in fields, roadside ditches and impoundments, rice paddies, streams, marshes, and riverbanks in West Malaysia away from the sea. I did not see a single individual in the 17 day field period. More specifically, not a single one was seen along the 122 km traversed of the Tembeling River, despite careful search for them. These birds are conspicuous in similar habitats in Africa and Central America. On the Sanaga River trip mentioned above, I photographed 7 species and saw at least 30 individuals. Such birds are a standard part of the scenery along large Central American rivers and in the kinds of habitats mentioned at the beginning of this paragraph. Inquiry of ornithologists in West Malaysia produced two useful comments. First, "they are absent because they don't migrate here"; well, what is wrong with West Malaysian real estate so that migrating large piscivorous birds don't use it much as overwintering grounds? Second, "these birds are conspicuous in areas near the sea." For example, Medway & Wells (1976) noted that 6 of the 9 resident species of Malayan Ardeidae are associated with mangroves. If in fact West Malaysia is a poor habitat for these birds, then the mangroves and river deltas should be the best of the sites, and appear disproportionately good compared to inland areas. Again, tiny Costa Rica has 14 species of resident Ardeidae (Slud, 1964) to compare with 9 for Peninsular Malaysia (Medway & Wells, 1976).

I hypothesize that herons, bitterns, egrets (and anhinga- and cormorant-type birds) are in short supply in the West Malaysian inlands simply because the waterways don't generate enough biomass of aquatic food for them. If the surrounding terrestrial habitats generate a reduced number of insects as well, which are an important part of the diet of many ardeids, the effect would be compounded.

The biomass of vascular epiphytes in the crowns of rain forest canopy-member trees at low and intermediate elevations is conspicuously lower in dipterocarp forests than in analogous rain forest in Costa Rica, Venezuela, Colombia, Cameroun (Edea Forest Preserve), and Uganda (near Fort Portal). The

quantity of bare horizontal large branches in the canopy of a forest such as that at Pasoh or Taman Negara is phenomenal.

I hypothesize that the cause is that the habitat generates such weak nutrient rain (bird droppings, dead insects, ant nest debris, rainwater minerals, dust, leaf and fruit litter, leachate from living tissues) that the epiphytes are starved off the tree. In short, I suspect that it is a general example of the extreme case at Bako National Park, Sarawak; here, on a white-sand soil area, the only surviving epiphytes on upland trees were those associated with the nutrient-gathering activities of an ant colony (Janzen, 1974c). There are several conspicuous alternative hypotheses as to why there is a shortage of vascular epiphyte biomass as compared to neotropical rain forest.

(a). The bromeliads (Bromeliaceae) never made it to the Malaysian tropics and it is their absence that makes epiphyte biomass seem so low. Such a hypothesis does not explain why epiphytic orchids, gesneriads, ferns, asclepiads, Piperaceae, ericaceous shrubs, rubiaceous shrubs, etc. are equally low in biomass.

(b). The Dipterocarpaceae, which make up 30 to 90% of the crowns in the canopy of the forests I examined, have evolved bark traits inimical to epiphytes. It is certainly possible for this to occur, as there are species of neotropical rain forest trees that regularly have crowns clean of epiphytes while growing only a few feet from many species festooned with epiphytes. However, if this is the explanation, it is many more species of tree than just those in the Dipterocarpaceae that have perfected their anti-epiphyte defenses. It seems unlikely to me that a whole flora of large trees could evolve this ability. Furthermore, if nutrients are exceptionally scarce for epiphytes, then even weak defenses may be adequate to keep them off.

There are two observations that are relevant to this hypothesis. On rare occasions I did encounter a native tree that was solidly covered with large epiphytes. For example, there is a medium-sized tree on the bank of the Tembeling River about halfway between Tembeling and Taman Negara that has hundreds of plants of a large basket fern on it (though perhaps it might be one huge clone linked by rhizomes). I saw no other individuals of this fern on the trees along the river. How does a huge plant like this one stay in the game as an epiphyte? It is possible that its litter-capturing leaves have an exceptionally robust ant colony living in them, or that its substrate tree is one of the few epiphyte-susceptible species in the region. Second, when Central American trees such as *Pithecellobium saman* (rain tree) or mahogany (*Swietenia* spp.) are planted in Malaysia, they develop large epiphyte loads. However, all the examples I saw were growing in small villages or roadsides where one would expect dust and other debris to provide high quality aerial fertilizer for the epiphytes. It is notable that these trees are deciduous forest trees in Central America and when transplanted to the evergreen forest within their native country, they also develop exceptionally high epiphyte loads, even for the rain forest.

In closing this section, let me call your attention to a quite different set of habitats where there appears to be a relationship between animal species richness and harvestable productivity. On Costa Rican and Venezuelan mountainside gradients, rather than the species richness of insects in sweep samples falling

off linearly with increasing elevation, it actually increases or at least stays about the same up to about 1,000–1,600 m elevation (Janzen, 1973a, Janzen et al., 1976). I have hypothesized that this "mid-elevational bulge" is the result of a similar bulge in harvestable productivity that occurs in the following manner. As one rises in elevation, the nights become cooler but the day does not cool as rapidly, and thus photosynthate production does not decline as rapidly as does nocturnal respiration. The result should be a greater amount of net produce per unit time for the plant, until an elevation is reached where diurnal photosynthesis is also severely reduced.

If this is actually going on, should it result in an increase in numbers of *species* of herbivorous insects? I would argue yes, because as I have argued earlier, there should be more fractions of each plant species (e.g., the new shoot tips produced in the lower outer third of the crown) that are large enough to support a specialist herbivore. By like reasoning there should be an increase in the species richness of arthropod predators and parasites of these insects (Janzen, 1973a, 1977c). The more generalized a feeder (e.g., birds as contrasted with parasitic Hymenoptera), the less a taxonomic group should be affected, but all should be affected somewhat. Moving in the other direction, should the increased photosynthate production result in more species of plants than expected with a straight-line relationship between elevation and harvestable productivity? Yes, but again to a lesser degree than with the herbivores. By increasing net photosynthate to an individual plant, there will be some kinds of specialization in which it can now participate (and thus more species can be packed into the habitat), but the relative heterogeneity of the increased photosynthate should be low compared to that received by the herbivore; the resource called sunlight is subdivided into many fewer compartments than the resource called "those plant parts that a herbivore eats."

By these varied examples I mean to suggest that a very promising yet unexplored area in tropical animal-plant interactions is the relationship between the pattern and amount of harvestable productivity and the numbers and kinds of animals present, and vice versa. We badly need solid data on relative abundances of animals and rates of production of harvestable parts of plants, collected with reference to particular questions such as "Given foraging inefficiencies and temporal distribution requirements, how much small bird biomass can be supported by the understory fruits of Pasoh rain forest?" Or, "Do mid-elevation plants replace shoot tips faster than their analogues at low elevations?"

MONOCULTURE FORESTS

In worrying about tropical forests, the intellectual interest of ecologists and population biologists has been largely focused on the "Oh My" habitats containing many species of trees (e.g., Ricklefs, 1977; Janzen, 1970; Connell, 1971; Ashton, 1969; Grubb, 1977). However, what I find much more perplexing are the lowland tropical forests with extremely low species richness of large trees: *Shorea albida* peat swamp forests in Sarawak (Anderson, 1961, 1964); *Mora excelsa* forests in Trinidad (Beard, 1946; Rankin, 1977); *Ocotea*, *Mora*, and *Eperua* forests in Suriname (Richards, 1952); *Gilbertiodendron dewevrei* forests

in West Africa (Gérard, 1960); mangrove forests around the world (Watson, 1928); *Strobilanthes* forests in the Asian tropics and bamboo forests around the world (Janzen, 1976b); *Raphia taedigera, Pterocarpus officinalis, Prioria copaifera,* and *Parkinsonia aculeata* swamp forests in Costa Rica (Janzen, 1977b and unpublished). For the mercenary at heart, esoteric ecological studies of these sites and their plant-animal interactions should tell a very great deal about the art of growing monocultures of tropical trees without a large input of pesticides, herbicides or other costs. Perhaps instead of worrying about the return to nature through the reinvention of mixed stands, which is so much in fashion these days, we should be studying much more intensely those species that naturally occur as pure stands. Not that I am eager to see this information become part of the foresters' operating protocol, however, unless it is accompanied by a (unlikely) kick-back to biology in the form of inviolate forest preserves.

The questions these pure stands bring to mind are numerous, and here I mention just a few.

(a). From whence come the pollinators when a large pure stand suddenly comes into flower, a pure stand that has had little or no flowering activity for one to several years? In general, these monocultures are adjacent to much more mixed stands of plants, and I suspect that it is from these stands that they draw most of their pollinators (though bamboo use wind and *Strobilanthes* use highly nomadic bees; Janzen, 1976b). In the specific case of Dipterocarpaceae, which form a "monoculture" of sorts in Malaysian forests if the entire family is viewed as a species, Ashton and his associates have found that the enormous quantities of flowers suddenly produced are probably pollinated by thrips (Ashton, personal communication), and I suspect that these insects feed on the vegetative parts of dipterocarps or other plants during the intervening years. Further, being very small, thrips can have a very high rate of population growth; the flowering season for dipterocarps as a whole is 4 to 6 months in length and thus there can be an extensive population explosion of thrips. Finally, it appears that the flowering times of the different dipterocarp species are scattered through the overall flowering time (in contrast to the highly synchronous fruit drop over about 2 months), and I suspect that this is the result of interspecific competition for pollinators (Janzen, 1977d).

(b). In every monoculture stand of tropical forest known to me, the usual dispersal of seeds is by falling below the parent, variously aided by wind; thus a shortage of dispersal agents would not appear to be a problem for these plants. However, this kind of dispersal means that a near neighbor is likely to be a sib, mother, grandmother, etc., and that outcrossing is therefore more difficult than in a population whose seed shadows overlap widely due to animal dispersal of seeds. But then again, in a permanent monoculture, perhaps the best genotypes are extremely specialized to that site, and thus genotype disruption or offspring heterogeneity through outcrossing and/or interspecific introgression is more disadvantageous than in a site that is more varied edaphically and more varied with respect to herbivore challenges.

(c). Why don't those herbivores that can deal with the defenses of monoculture tree stands move into these habitats and literally mow them to the

ground? There is certainly no escape in space. There are herbivores that can feed on the vegetative and reproductive parts of these plants (e.g., Anderson, 1961). I suspect that the answers to these questions are in the following area. When the habitat first appeared, and various species of trees were specializing with respect to it, those that got mowed down when they occurred in pure stands probably dropped out of the race early on (they should still persist in mixed stands, however). Second, one of the traits for living in a habitat supporting a pure stand should be the evolution of those kinds of chemical and behavioral defenses so effective that the plant does not rely on escape in space; perhaps they are more expensive chemically, but then again perhaps they can be afforded owing to less investment in interspecific competitive ability (e.g., desert cacti). Third, these plants have escape in time, and they use it; in many species seed production is highly synchronized within the year and in many species, at supra-annual intervals (bamboo being the epitome; Janzen, 1976b). Owing to the extreme specificity displayed by many tropical seed-eating insects, the seed crop of the monoculture stand does not necessarily draw a guild of insect seed predators in the same manner as the flower crop may draw a guild of flower visitors from the surrounding mixed forest. However, such plants may also be involved in satiation of seed predators, and then they may draw large numbers of animals from surrounding areas and require long supra-annual periods to accumulate enough reserves for enough seeds to satiate these animals (e.g., bamboo, Dipterocarpaceae). The same process is likely to be operating with new leaf production. For example, in Corcovado National Park (Costa Rica), all trees of *Mora oleifera* drop their leaves in late November and put out a new synchronized crop in December.

Secondary Compound Chemistry and Herbivores

This is undoubtedly the most actively expanding area in tropical (and extratropical) animal-plant interaction studies. It is easy to predict that the descriptive data and tests of hypotheses over the next ten years will make our current understanding seem amazingly primitive and naive. Take any paper on this subject in a current journal, and you can generate more questions with its data than it answers; and if not, just combine it with the next apparent test of the same hypothesis to get the desired effect. We are even still drowning in terminological difficulties, with specialist, generalist, secondary compound, herbivore, strategy, community, at the top of the list; at least we seem to have left niches by the wayside.

It is presumptuous for me to finger promising areas, but since asked, I will presume. As I mentioned earlier, do not jump on me for leaving out yours, just be happy that it is not yet a bandwagon. I will simply ask questions, the answers to which I feel are either as yet invisible or are only dimly visible.

(1). What sort of enzyme systems occur in the guts and livers of herbivores (e.g., Freeland & Janzen, 1974; Krieger et al., 1971), and can they be turned on and off so fast that an animal can move from one species of plant to another with hardly a pause? Yes (Brattsten et al., 1977). If they have them generally,

and can be so activated, why aren't all animals generalists that can feed on any kind of foliage?

(2). Is it true that large animals mix their foliage intake as a way of minimizing damage from any one secondary compound (dilution, antagonisms, keeping each compound at a low concentration), or do they do it largely for nutrient balance reasons (Westoby, 1974; Freeland & Janzen, 1974)?

(3). There is more foliage present of species that big herbivores are known to eat than they do eat; does this mean that they are not food-limited (Berwick, 1974), or does it mean that there are upper limits for even the acceptable items? Or does it mean that the critical times in food shortage (pregnancy, weaning, etc.) have not been examined?

(4). How do the metabolic costs of making secondary compounds (Penning de Vries et al., 1974) compare with the fitness costs of making them?

(5). At the habitat level, what is the structural array of secondary compounds? In other words, are defenses more heterogeneous within than between the food of herbivorous guilds (Janzen, 1973b; Feeny, 1976; Rhoades & Cates, 1976; Cates & Rhoades, 1977; Futuyma, 1976)?

(6). Why do many plant parts contain trace amounts of a variety of secondary compounds, and then a large amount of a few? Are they really sloppy or does this array present a more viable or effective defense against the more specialized or the more generalized animals?

(7). How would you design the optimal pathway for the production of a secondary compound? Example: minimize the number of places that enzymatic reactions are needed, maximize the number of times that the same enzyme can be used, canalize the substrate-product sequence such that its intermediate parts cannot be stolen from other pathways (but perhaps a really sophisticated system would allow borrowing?).

(8). Why are specialist animals specialized to only one kind of host (if they are); is it that detoxification systems are really that intersystem incompatible? Or is it like the canavanine system where the beetle is using that which is produced by the detoxification process (Rosenthal et al., 1977), and therefore we can state that the animal avoids other hosts not only because they are toxic but because they do not offer special dietary input.

(9). Why are sugars the molecules tacked onto large active molecules to render them inactive (e.g., lectins, Liener, 1976, and other glycosides)? Is it just because of the ubiquity of hydrolyzing enzymes in animal guts?

(10). Since insects have a much shorter generation time than do plants, why don't insects always come up with a resistant strain that eliminates the plant before the plant can evolve a chemical defense?

(11). What happens when we view cellulose as a secondary compound?

(12). If bacteria can degrade cellulose, lignin and other such indigestibles, why can't animals do the same?

Why do Fruits Rot and Seeds Mold?

The brewery's fermentation vats are not where yeast evolved ethanol produc-

tion and bread is not the native habitat of blue bread mold. An exploration of the biology of rotting fruits and molding seeds is likely to produce some very interesting and unexpected results, both here and in the tropics. When a microbe has found itself a ripe fruit, it has two options. It can begin using the resource rapidly and directly for its own growth and multiplication. On the other hand, it can do this somewhat more slowly and convert part of the resources into compounds which the anticipated vertebrate consumer of that ripe fruit will find objectionable, toxic, repulsive, etc. I suspect natural selection to have favored genotypes displaying the latter solution. The selection should be more intense the more rapidly the dispersal agents and fruit parasites remove the fruits from the tree, and the less fastidious are the frugivores. Seen in this light, a sour or alcohol-rich fruit is not just an accident of microbial metabolism or the detritus of microbe-microbe warfare, but may also be the explicit outcome of selection for avoidance of consumption of microbes (or insects) by vertebrates (Janzen, 1977f).

The same argument may easily be applied to the fungi whose hyphae grow over the surface of grain caches of man and other animals. Only here, they are protecting a much more valuable resource (higher nutrient content, lower abundance, large amount of work invested in harvest is a measure of work that will have to be repeated to reharvest it if lost, reserves for a resource-poor future, etc.). The protection will have to be more violent than for a fruit, and it is; aflatoxins, ergot alkaloids, and antibiotics may be used as examples. It is of particular interest here that both insects and vertebrates are susceptible to these compounds, and the only fungal hyphae that regularly make such nasty things are those that live on grain stores (Janzen, 1977f).

The biology of rotting fruit and moldy grain stores in the tropics is unknown in the wild and in most human habitats. Why do cassava tubers (Manihot) spoil so quickly that a major portion of the earth's cassava production land is serving as a storage bin because once harvested, cassava tubers have to be eaten? Another way to ask this is "Why do the spoilage organisms in cassava tubers so quickly render them unuseable for vertebrates?" Many species of tropical fruits are notorious for being poor at shipping and storage, unless picked extraordinarily green. Is this because the fruits are particularly susceptible to rotting organisms (owing to lack of selection for long half-life of ripe fruits owing to very active dispersal agent guilds), because tropical microbes are especially competent in their competition with vertebrates (owing to very active dispersal agent guilds), or a combination of the two? How long does a yeast clone have to make a tropical rain forest fig so sour that a bat will leave it on the tree? Perhaps it may have only one or two days at the outside. I should add that the opportunities for coevolution of competitive partners against the vertebrates is very great, and may take the form of teams of microbes and the insects that carry them from rotting fruit to intact ripe fruit. It is even possible that an exploration of some of these esoteric areas might well lead to pragmatic applications in the area of Ashton's (1976) proposals for exploitation of wild tropical fruit trees for their fruits.

There Is No Optimal Seed

The fitness of the female parent tree has to be measured in some way relevant to the number of new members she contributes to later generations and how well these new members do on the same parameter. The environmental challenges presented to her seedlings are varied and unpredictable with respect to any given seed (though the variation and relative abundance of environmental challenges may be quite predictable to the parent). There can therefore be no optimal seed size for any species of tree. A large seed may generate a very strong seedling, but it may be sorted out by the seed dispersal process so as to land in a poor site. A small seed may generate a puny seedling but regularly land in a heavily insolated site. This year, a female may have ⅔ of her seeds land on dry sites and ⅓ on wet sites; next year she may do the opposite purely because of interyear differences in weather. In view of these problems, I hypothesize that there can only be an optimal distribution of seed weights within a female's seed crop. If this is so, then the distribution of weights of seeds (or some other measure of the size of the bag lunch for the seedling) is not a simple outcome of sibling competition and physiological sloppiness by the parent plant, but rather may also be engineered by the adaptive value of having various proportions of the seeds in different weight classes. Incidentally, since the challenge to seeds varies from year to year, there may not even be an optimal seed size distribution in a crop; it will have to be within a lifetime.

Ateleia herbert-smithii, a caesalpinaceous legume tree in Santa Rosa National Park, Guanacaste Province, Costa Rica, may provide an example. Not only does this tree display 1.89-fold variation in the mean seed weights among trees, but within a crown there is 1.6- to 2.6-fold variation in seed weight. There are some cases where twins are produced in the normally single-seeded wind-dispersed fruits. Here, the pair of seeds has a combined seed weight greater than the mean weight of solitary seeds, but each twin weighs considerably less than the individual solitary seeds. This can be simply interpreted as the outcome of sibling competition. However, it could also be a mechanism for dropping some light seeds near the parent plant. A fruit with twins should fall in that part of the seed shadow that normally receives single-seeded fruits with heavy seeds. In fact, the production of twins may be adaptive simply in homogenizing the seed shadow (Janzen, 1977h). In the same vein, the 3.62-fold variation in seed weights found within a single crop of *Mucuna andreana* could well be adaptive in generating a more homogeneous seed shadow than if all the seeds weighed the same (Janzen, 1977g).

A small hard object moves through the digestive tract of an animal at a rate related to the object's volume, shape, specific gravity and (probably) surface texture (Hoelzel, 1930; Alvarez & Freelander, 1921; Hinton et al., 1969). It follows that if a vertebrate eats a distribution of seed sizes from a single crop, they are likely to come out in a different pattern than they went in. Further, the probability that they will go in at all should be influenced by these traits, as well as the relative seediness of the fruit. For example, does a tapir spit out flat 500 mg seeds more frequently than spheroidal 500 mg seeds of the same species? Does a deer chewing its cud spit out the large members of a seed crop and let the

small ones pass on through? Could the small seeds from the same *Enterolobium cyclocarpum* seed crop crack between the molars of a peccary more easily than the large seeds? Yes (Janzen & Higgins, 1977).

Once we put on this pair of glasses, interesting variation pops out all over the place. What is the meaning of variation in fresh ripe fruit weight within a tree's crop? Bonaccorso (1975) noted that different species of bats took *Ficus insipida* fruits of different weights from the same tree; this should generate a quite different seed shadow than if all the figs were of the same weight and thereby taken by only one species of bat. What is the significance of the spatial variation in fruit location in the crown? What is the significance of the temporal variation in fruit ripening times within the crown? What about the variation in seediness within a crown?

But do not forget the zygote. The world is not constituted solely by female parental manipulation. What is good for the parent is not necessarily good for the individual seedling. Once the zygote is formed, you might argue that it should do everything it can to extract as many resources as possible from the parent plant. Of course, the parent has many physiological ways of controlling this, but there may also be good reasons for the offspring to constrain its gluttony. For example, the very large seed may simply be spit out below the parent by the dispersal agent, and its less greedy sibs make a happy passage through the intestine to a distant light gap. The large seed may lower its fruit/seed ratio to where it is taken late if at all, and thus be killed by some seed predator taking what has been left behind by the dispersal agents. The individual zygote is not in the process of generating a seed shadow but rather in maximizing its own chances of survival to a highly reproductive adult; it has only one chance, the parent has many.

Optimal Mate Selection

Animals are conspicuous in their courtship displays, fickleness, promiscuity, coyness, variably intense rape, and other descriptors of mate selection by both sexes. What are the analogous processes in plants? I would like to suggest that they are choice of pollinators, timing of flower presentation, duration and time of stigmatic receptivity, duration and time of pollen release, degree of separation of the sexes within and between conspecifics, abortion of ovules, and abortion of zygotes of a variety of ages. The core questions are "How many of which fathers does the female part of the plant genome want for any given seed crop?" and "How many offspring in which and how many seed crops does the male part of the plant genome wish to sire?" I would argue that in either case the answer is not a maximum number but rather some optimal number and optimal distribution. Further, I see no reason to believe that the optimal numbers and distribution of fathers and mothers are very likely to be the same for the female and male, and that the difference leads to such things as differential pollen acceptance, selective pollen presentation, monoecy, dioecy, etc. (Janzen, 1977a).

I suspect that the most unappreciated mechanism for shaping the genetic composition of her seed crop is that of zygote abortion. It is conspicuous that the individuals of a very large number of species of plants regularly abort all but a

very small number of the flowers that they produce. Flower to mature fruit ratios of 100–500 to 1 are commonplace in large tropical trees. Even careful hand pollination does not drive this ratio downward, though it can in certain species. Incidentally, I should note that pre- and post-zygotic abortion are probably not as different as they would seem since both should be controlled by the seed-bearing plant. The male portion of the zygote is certainly not going to be selected for abortion tendencies as it has all to lose and nothing to gain.

Since my focus is here on animal-plant interactions, let me list some of the ways they influence abortion of flowers and zygotes.

(a). By attacking a fraction of the ovules and zygotes in the flower and developing fruit, seed predators may render the fruit not "worth" the cost of further development or maturation.

(b). By being unpredictable in which flowers or immature fruits they will attack, and to a certain degree in how many, such animals require the retention of a large number of (perhaps) suitable flowers or green fruits from which the fruits to be matured can be selected after the animals have taken their toll (the excess flowers or fruits are then aborted).

(c). By bringing variable amounts of appropriate pollen (e.g., pollen that is not from yourself or a close relative) to the stigmas, the pollinators require the production of a large number of stigmas so that at least some minimum number get the right amounts of the right pollen; the flowers containing stigmas with the wrong pollen are aborted.

(d). Owing to the vagaries and resource-gathering behavior of visitors to flowers, a large flower crop may be necessary just to satiate visitors, to get the right kinds, and to do it in competition with other plants; these flowers are then aborted simply because insufficient resources can be spared to mature their seeds even if pollinated.

Viewing pollen donation and capture in the light of these comments brings me to the problem of the act of not setting seed by a flowering tree. With dioecious species, the lack of seed production by male trees has never caused the puzzlement it is due (but see Bawa & Opler, 1975, 1977). Dioecy is just a more final example of the behavior displayed by a tree with perfect flowers that likewise sets no seed. I would hypothesize that such trees, dioecious or hermaphroditic, have often made some kind of an internal decision that they will have a higher fitness by putting everything into pollen donation rather than into pollen capture and nursing zygotes. Medway (1972) recently commented on how "after flowering, invariably some species failed to produce fruit"; Grubb (1977) picked this up as "circumstantial evidence exists for massive failure of pollination in some species . . . in the lowland tropics"; it is commonplace for foresters to label trees that flowered but did not seed as having "failed" to reproduce. Quite the contrary, they may have reproduced much more heavily than the tree bearing seed, simply by having sired many seeds on that tree and others that did set seed. We don't label an animal as having failed to reproduce because he doesn't get pregnant after copulating.

There are at least two ways that animals may be responsible for morphologi-

cal or physiological dioecious behavior by plants, both of which deserve much more attention than they have received.

(a). If seed predators and their satiation are involved in the tree's biology, the tree reproducing by seed may have to produce a very large seed crop or none at all; here then, the highest fitness may be achieved by being solely a pollen donor when young, sick, or between large seed crops.

(b). Dispersal agents may not be accurate enough to put more than an occasional seed into a habitat in which there are enough resources to be a healthy seed-bearer, but may place many seeds in habitats that just barely allow adult survival. The plant, once dispersed to the latter habitat, cannot get up and walk to a better place, and thus may be doomed to be a pollen donor or nothing.

Complex Animal-Plant Interactions

There are four complex animal-plant interactions about which we now know a fair amount: orchid-euglossine bees, figs-fig wasps, neotropical acacia-ants, and leaf-cutter ants. Their taxonomy is fairly well understood, the basic elements of the interaction are understood, and they have been widely publicized. On the one hand, it appears that there is little interesting new ground to be plowed with each, and therefore the bright young field naturalist should look for other systems on which to expend energy. I would contend the opposite. These systems are now prime for high quality field studies incorporating modern ecological and population biology thought; the student need not waste years doing their taxonomy and natural history just to determine where to start. I have not started such a new study with any of the first three, but by nibbling at their surfaces for just a moment, the following interesting areas appeared. The fourth is being heavily studied by several investigators and I will not dwell on it here (e.g., Rockwood, 1975, 1976; Cherrett, 1968; Martin, 1974; Lugo et al., 1973; Hubble, personal communication).

orchid-euglossine bee interactions

(a). How many parasites of the system exist (analogous, for example, to *Pseudomyrmex nigropilosa* in acacia-ants (Janzen, 1975a) or to *Sycophagus sycomori* in *Ficus sycomorus* (Galil et al., 1970)? It is assumed that the bees that come to the orchids and to the scents put out to survey them are pollinators of one or more orchids. There is no biological reason why this has to be so. Even if the bee does pick up pollinia, there is no guarantee that it has the appropriate behavior and/or morphology to put it back in the right place. It is already recognized that a visiting euglossine may not be the pollinator, yet get chemicals from the flower (Dressler, 1968a; Dodson et al., 1969); however, there is no reason that such a bee has to be the pollinator of *any* orchid. However, there are obvious forces operating to set the carrying capacity of the habitat for such parasites, and this should vary with the number of species of orchids, the number of species of euglossines, their numerical relationships, seasonality, etc.

(b). Is the visitation of an orchid's flowers, in its natural habitats, habitat-

independent? Some observers have already noted that certain orchid bees will not come to baits or orchids placed in the open sun but will visit them in the shady nearby rain forest understory. I suspect that the story is much more complex than that, and much more interesting. In March 1977 I put five different chemicals (cineole, eugenol, methyl salicylate, benzyl acetate, and methyl cinnamate) out in five different forest types on the same day within a circle of 2 km radius in Corcovado National Park, Costa Rica. The numbers of euglossines that came to each site differed dramatically and the array of species differed somewhat, suggesting that if any given orchid were growing in one of these sites, its visitors could have been dramatically different. An orchid is not an orchid is not an orchid. Such differences should have dramatic effects on species packing in orchids, inter-habitat species richness of orchids, and the relative fitness of an orchid in a given habitat as compared with a conspecific in another nearby habitat.

(c). How much self-pollination occurs in hermaphroditic euglossine-pollinated orchids by the simple event of a bee picking up a pollinarium today and bringing it back tomorrow? At least one tropical orchid, *Encyclia cordigera*, is highly self-compatible (study in progress, Santa Rosa National Park, Guanacaste Province, Costa Rica). Since most adjacent conspecifics are probably closely related (orchid seed shadows are probably strongly peaked as in other wind-dispersed seeds), there is also likely to be an extraordinary amount of incest in orchid matings.

And if interspecific hybridization occurs *physiologically* so easily with orchids (Dressler, 1968b), does this really mean that they have extremely faithful pollinators as is generally assumed, or does it mean that orchids live in a world where it is very profitable to steal genetic information as whole blocks or as proven mutations from other genomes? If they do the latter, then I expect strong selection for the ability to obtain this information without severe perturbation of the phenotype. The conventional means for detecting hybrids, the means that are used to say that orchid hybrids are very rare in nature, might be therefore of little or no use.

(d). An orchid female generally has fewer fathers for her clutch than does a member of any other family except perhaps the Asclepiadaceae (and speaking of which, what do orchids and asclepiads ecologically have in common so as to have generated their convergence on this axis?). Every orchid fruit, with its hundreds of thousands of seeds, has but one father. Depending on the behavior of the orchid bees and the density of orchids in the area, even if there is more than one pod per plant, it is possible for multi-podded clutches to have only one father. At the very most, the ratio of fathers to seeds has to be on the order of a very few to hundreds of thousands. In what way could this observation be related to the point made in the last paragraph of the previous section?

FIGS-FIG WASPS

(a). Since no one has ever done anything but rear the fig wasps out of syconia (and none of that has been done in a quantity any greater than that needed for taxonomic purposes) (Hill, 1967; Ramirez, 1970a), there is no infor-

mation on what kind of interspecific pollen is being carried *into* a fig crop. Again, the literature loves the statement that hybrids of figs are very rare (e.g., Hill, 1967); however, since there is only one experimental cross on record (Condit, 1950) how is one to know what a hybrid fig looks like? An extensive examination of the remains of the female fig wasps inside a large number of recently pollinated but still quite immature syconia would tell how much foreign pollen is getting into the system at each generation.

(b). Female fig trees pay offspring for pollination. Fig wasps are seed predators. There is no published study of the intensity of this predation, but one in progress shows 30 to 50% for three fig species. What is the possibility that one of the selective pressures favoring gynodioecious figs (one morph of the population has syconia with solely female florets with styles too long for oviposition) is the act of obtaining the services of the wasp without paying the cost in zygotes? What is the overall cost in zygotes per intact seed for monoecious as compared with gynodioecious fig species?

(c). Who eats figs? Everybody does. Nonsense. Yes, there are fig species that produce large numbers of small figs that are taken by a very large disperser coterie. These species must have very homogeneous seed shadows (generated by birds, bats, pigs, primates, etc.). On the other hand, there are fig species that seem to be largely visited by a very select subset of the frugivores in the community (e.g., *Ficus ruginervia* produces large figs apparently taken only by gibbons, siamangs, and two species of squirrels when growing only a few meters away from *Ficus sumatrana* which was visited by at least 25 species of birds and 9 species of diurnal mammals—to say nothing of bats, which were apparently unrecorded; McClure, 1966). Morrison (1975) noted that the ripe figs of several species of Barro Colorado Island figs were taken largely or exclusively by bats; the howler monkeys are the only other visitors mentioned, and they appeared to take largely immature syconia. It is my guess that they took almost entirely immature syconia.

I suspect that the traits of ripe fruits are engineered by the need to keep them out of the wrong dispersal agents as much as to get them into the right ones (and see Howe, 1977). There should be many parasites present in any disperser-fruit system. The trick is recognizing the parasites (as separate from the seed predators) because they do their damage by putting the seed in the wrong place, rather than by killing it directly. The neotropical oil birds (Snow, 1962) come to mind as the most glaring example, since it appears that many of the seeds they eat are later regurgitated in a cave where they die. Likewise, a Mexican oriole that eats the fruit pulp around *Acacia cornigera* seeds and drops the seeds below the parent tree may have killed those seeds as dead as if it had ground them in its gizzard. It appears that *Andira inermis* fruit pulp may contain an antibiotic which thereby renders it a high quality food item solely for those animals that depend little on bacterial degradation for the extraction of nutrients from their food (Janzen, 1977e). It occurs to me that the various bat-dispersed figs on Barro Colorado Island may be doing the same; interestingly, such a compound might also be functional in slowing the rate of spoilage of a fig that has already been opened to the outside world by the exit of the fig wasps. If this

hypothesis is correct, then consumption of green figs before such a compound is activated might be the only way that a howler monkey can eat them, since it depends heavily on its bacterial community for degradation of foliage. Howler monkeys often avoid ripe fruits but eat the same species when green (Glander, 1975a, 1975b, 1977).

(d). The current consensus seems to be that fig wasps are very host-specific and that the figs are strongly synchronized within a given crown (Ramírez, 1970b; Hill, 1967). I have no doubts that this is the case for many species in many habitats. However, Ramírez (1970b) has already pointed out that on islands there may be selection for the loss of synchrony within a crown if the fig population is so small that there could be times when no tree is in a receptive state. There should be other habitats where both the host-specificity and the synchrony should break down. Butcher (1964) stated that the two native species of *Ficus* in Florida, *F. aurea* and *F. laevigata,* are pollinated by the same species of wasp, *Secundeisenia mexicana.* If this should occur anywhere, it should be Florida with its killing frosts. McClure (1966) noted that in the dipterocarp forests around Ulu Gombak there was a two month progression of ripe figs through the crown of a *Ficus sumatrana* (and shows it in the graphs for two other species as well). Fig wasps take about a month for a generation. Unless the pollination is synchronized but the syconial ripening grossly asynchronous, there is a very great possibility of self-pollination in these species of figs. At least two selective pressures could be operating to produce asynchrony within the crown. First, it may be that fig tree density is generally low in this forest, perhaps even as low as on a small island from the viewpoint of the wasps. Second, it may be that the actual biomass of fig-removing animals is small, and if all the figs this tree can make in a pulse were to be matured in a week or two, most would rot on the tree or the ground for want of not having been removed (the frugivores having been satiated).

ACACIA-ANTS

(a). There is no wild plant species anywhere in the tropics for which even an approximate herbivore load has been described. If the ants are removed from neotropical swollen-thorn acacias, the herbivores that normally feed on them and those that feed only on the largely undefended plants often become temporarily abundant and easy to census. Combined with careful observations of the insects feeding on acacias with their colony intact, it would be possible to not only rapidly identify the herbivore load of at least one plant species, but to ask how it behaves when the defenses of the plant are suddenly removed without physiologically altering the plant. When my early ant-acacia studies came out, there was a good deal of "Oh My" of how all those little ants could do such a marvelous job of defending the tree. The significance of those studies lay not, it seems to me, in this aspect. Rather, here we have a plant that in nature can be deprived of its defenses and thereby demonstrate how important are its defenses in determining the amount and structure of the herbivore load.

(b). When an ant-acacia is crossed with a non-ant-acacia, the offspring are most amazing organisms. They have either Beltian bodies, large to normal

thorns, large nectaries and seem to be poorly protected, or they almost entirely resemble the non-ant-acacia parent. Thus it is as though the ant-acacia traits were one gene (and you get an ant colony as well). If this gene is donated through interspecific introgressive hybridization, a non-ant-acacia may become an ant-acacia. It does this without ever losing its other traits which, for example, would cause it to be placed in a quite different subgroup of the genus. It would then appear that the ant-acacia interaction had evolved independently on several different occasions. The 10 or so species of neotropical ant-acacias seem, on the basis of flower and fruit traits, to belong to quite different species groups (Janzen, 1974d). The system is wide open for experimental verification. And what would it mean to attempts to reconstruct phylogenies based on suites of traits?

(c). There are three species of obligate acacia-ants in Guanacaste Province, Costa Rica, that protect the common swollen-thorn acacia, *Acacia collinsii* (*Pseudomyrmex belti*—black; *P. nigrocincta*—the smallest of the three and with a yellow body with the gaster held straight out in back; *P. ferruginea*—rust red with the gaster commonly curled under the posterior part of the thorax). They all eat the same thing (Beltian bodies and foliar nectar), live in the swollen thorns, and aggressively protect the plant. All three occur in every habitat I have ever sampled. No large colony will cooccur in the same acacia with another colony. All colonies have but one queen, and while many queens may start out in the same acacia seedling, the winner takes all. It is hard to imagine a more monomorphic resource than ant-acacias. I suspect that originally one species was a specialist on the ant-acacias in the forest understory (*P. nigrocincta*), one species was a specialist acacia growing in open but moist sites such as river edges and marsh edges (*P. belti*), and one species was a specialist on acacias growing in fully insolated but very dry sites (*P. ferruginea*). When the pasturing, cropping, and timbering broke up the habitat structure, all three species moved into each other's habitats and are found there today. In contemporary habitats the ratios of the species vary widely among habitats, and I suspect that in the original habitats there were always a few colonies of the other two along with the most abundant species. The colonies can be moved about, the acacias can be seeded with queens, and all occur in large numbers. The opportunities for experimental study of direct competition between sessile animals in terrestrial community are enormous.

(d). The pulp around the seeds of *Acacia collinsii*, moist when ripe, can be placed in a plastic bag, sealed, and left for a year without spoiling. From what I said earlier about bats and *Andira* and fig fruits, there is one obvious suggestion about what it contains. All swollen-thorn acacias have seeds imbedded in a sweet pulp (Janzen, 1974d), apparently for seed dispersal by birds (in contrast, I know of no neotropical non-ant-acacia with this trait). Presumably this trait arose many times independently. What a marvelous opportunity to study convergence in fruit protection traits.

The above hypotheses and systems briefly alluded to for orchid-euglossine bees, figs-fig wasps, and ant-acacias are, I am certain, only a tiny fraction of the studies that can be developed into large and clean studies in coevolution, popula-

tion biology, gene flow, competition, etc. These suggestions are possible because some background has now been developed for these systems. Yes, the "Oh My" part of the studies has been killed rather dead; now it's time to start on the interesting things.

One Liners

(1). Why do trees have rotten cores? Hypothesis: to provide a place, through the removal of unneeded structure, for animals to roost and defecate and for microbes to grow, which in turn generate a nutrient pool for the tree's roots. The actual process should be through the selective and only temporal protection of the core of the heartwood from decomposers (Janzen, 1976c; Fisher, 1976; Thompson, 1977).

(2). Why do vertebrate dispersal agents leaves the tree to eat the fruit they have picked? Hypothesis: because there has been strong selection for chemical, morphological, and behavioral traits of the parent tree to be an objectionable place to perch. The competing hypothesis is that the fruiting tree is a focal point for foraging carnivorous predators.

(3). Why don't the ants of the world take over the flowers of the world and protect their nectaries just as they do extra-floral nectaries (even on those on the outside base of the flowers)? Hypothesis: there is an anti-ant compound generally present in floral nectar. And in case you still think nectar is just sugar water, read recent papers started off by the Bakers (Baker & Baker, 1975; Baker, 1975).

(4). Why do rain forest seedlings with mycorrhizae recover from herbivory much better than do conspecific seedlings that have not yet acquired (accepted?) a mycorrhizal association? Hypothesis: the seedling can mark time waiting for the appropriate fungal associate using only its seed reserves plus the very small amount of resources it can harvest in the heavily shaded rain forest understory, but if it has to undergo the major capital investment of replacing lost photosynthetic structures, it does not have adequate resources (Janos, 1975).

(5). Why do rain forest understory shrubs contain a high amount and diversity of so-called trace elements (boron, cobalt, etc.; F. Golley, personal communication). Hypothesis: the heavily shaded rain forest understory is one of those resource-poor habitats where chemical defenses are of utmost importance (Janzen, 1974b); large quantities and many kinds of secondary compounds may require large quantities and many kinds of co-enzymes for their protection, and co-enzymes normally contain a molecule of a so-called trace element.

(6). What is the distribution of intensity of seed mortality by animals among the members of a tropical tree population? Hypothesis: there is a very skewed distribution, with most individuals producing few or no surviving seeds, and a very few producing most of the members of the next generation. If this is verified, then the opportunities for rapid genetic change and the selection for high levels of information exchange among members of the population should be very high.

(7). What do whole disperser coteries, herbivore loads, and suites of pollinators for an individual and a population look like? Hypothesis: they will be

rich in species that parasitize the system, rich in species that gain resources but take so little that the mechanisms to remove them would cost much more than the value of what they take, have a few key species that drive many of the traits of the system, treat individuals very differently even within populations of closely adjacent individuals, and display strong competitive interactions through the medium of the plant (Janzen, 1973c), as well as directly with each other.

(8). Why are grasses so edible? Hypothesis: they are involved in satiation of leaf predators (being possible by having put the high investment centers underground where they cannot easily be reached by fire and herbivores); the cost of chemical defenses would generally be higher than the fitness loss that occurs through the grazing that is produced by the animals that make it from one rainy season to the next (and see especially Sinclair, 1977).

(9). Are plant apparency arguments (Feeny, 1976; Rhoades & Cates, 1976) applicable to all parts of plants, as they appear to be to foliage? Hypothesis: probably, but it will require some very careful definitions of what is apparent and what is not. For example, at least two major groups of mast-seeding trees, oaks and dipterocarps, have polyphenolics as their major chemical defenses (if any be). A very large number of trees that do not display habitat-wide supra-annual synchrony of seed production have alkaloids and other conventional toxins in their seeds. One could argue that the seeds of mast-seeding species, widely spaced in time, are less apparent than the seeds of tree species that fruit or seed every year. However, I could rebut this argument by noting that when the mast-seeders do seed, they do it in such abundance (and often in such pure stands) that the seeds are enormously apparent; on the other hand, species of seeds defended by alkaloids, etc. are often very widely scattered or rare, and thus much less spatially apparent, even if they fruit every year. In closing this section, I must note, however, that many species of seeds contain both direct toxins (alkaloids, uncommon amino acids, cyanogenic glycosides, etc.) and digestion inhibitors (tannins, lectins, protease inhibitors); e.g., chocolate beans contain tannins and 3 kinds of alkaloids. Perhaps it is that as the nutrient content per bite of food rises, the adequacy of only one class of defense in the plant part declines precipitously.

(10). Why is the biomass of palms in Africa so low? The exceptions are oil palm (*Elais guianensis*) and raphia palm (*Raphia taedigera*) pure stands in swamps, borassus palms in very arid areas (e.g., Samburu National Park, Kenya), and very thorny climbing palms in swampy rain forest. Richards (1973) has already noted that Africa has a ridiculously low number of species of palms—about 50 species as compared with about 1,140 in the neotropics and 1,150 in the Asian and Australasian area. Hypothesis: palms, with their single large growing points, are particularly susceptible to herbivory by elephants, mammals which were until recently prominent browsers in African forest habitats.

(11). Can the fitness of a plant be raised by herbivory, thereby selecting directly for palatability or lack of defenses in a plant part? This hypothesis has recently been championed by Hendry et al. (1976), Owen & Wiegert (1976), and Harris (1973), among others. Aside from the obvious cases of seed dispersal and pollination systems, and the problems of defenses in these systems being incom-

patible with "allowing" herbivory by the "appropriate" animals, I have yet to see a convincing case of a positive answer to this question. Of course, an herbivore may remove a part that would otherwise have to be actively dehisced by the plant, or turned off by the plant, but to put such an activity in the hands of the herbivore requires that it will only do that and that it will be reliable in its activity; that is to say, the plant loses part of the control over itself. In the most dramatic case, mild defoliation of crop plants may result in overall increased yield per field (Harris, 1973). However, this is quite easily explained by assuming that the defoliation breaks apical dominance, something that would result in loss of status in the natural competitive situation, but is optimal for properly spaced plants in the field situation. The same applies to cases where mild browsing of bushes appears to raise their vegetative productivity, and when mild defoliation of a wild plant increases its seed production (e.g., Cavers, 1973). In short, just because a person runs faster after hitting a wasp nest, we do not conclude that (a) being stung raises your fitness and (b) susceptibility to being stung is a mechanism evolved by humans to get themselves to run. Finally, I can simply state that the various schemes frequently proposed for the "value" of herbivores to the ecosystem at recycling leaf contents are evolutionary nonsense. There is no evidence that a plant gains more from having its leaves eaten and then (perhaps) taking up some of the mineral contents of that leaf or feces from the litter below than from keeping its leaf intact in the first place.

(12). Are extant gymnosperms and other "primitive" plants really freer of herbivores than are angiosperms (Regal, 1977)? If so, is this due to their secondary compound chemistry or is it due to accidents of host location by herbivores? Are we seeing the bare remnants of a once great flora being pushed out by the combined actions of herbivores and competition from plants with a superior growth form?

(13). Prominent and severe defoliation by highly host-specific Lepidoptera and Coleoptera occurs during the first 1–2 months after the rainy season begins in the Costa Rican lowland tropics (see Rockwood, 1973, for examples of its effects). Hypothesis: the cessation of defoliation after a single generation of a given species of herbivore is due to the accumulation of secondary compounds (such as digestion inhibitors, see Feeny, 1976) in maturing leaves which makes them unavailable to the insects. The corollary of this would be that a tree is susceptible to this event only because it has to make a new crop of leaves each year. Opposing hypothesis: the cessation of defoliation after a single generation of herbivores is due to a buildup of parasites and predators at this time of year. There is no direct or circumstantial evidence to support this hypothesis.

(14). New leaf-cutter ant fungus gardens are established by vegetative propagation from cuttings carried by the newly mated queens. Hypothesis: over many generations of leaf-cutter ants in an area, all the colonies will eventually be owned by the same subdivided individual fungus, which should in turn be the genotype that does best on that particular mix of plants which are available to the ants. This then becomes the world's largest fungus and uses armies of leaf-cutter ant colonies to feed itself; will this result in manipulation of the colonies at a density and degree of intercolony aggressiveness which is suboptimal

for the ants and optimal for the fungus? Does this mean that leaf-cutter ants are more finely tuned to a habitat than expected, and therefore will also have more than the expected difficulty in colonizing new habitats?

(15). It appears that the species richness of herbivore loads of perennial plants reaches an asymptote within a few hundred years after the species has been introduced, with the level set largely by the areal extent of the population (Strong et al., 1977). Hypothesis: this conclusion will be most robust with highly apparent plants that are generally defended by digestion-inhibiting chemicals, since it is these plants that will have the most in common with those native plants that are fed on by generalists; newly introduced herbaceous and other plants defended largely by more direct toxins should require considerably more time to accumulate a normal herbivore load from the indigenous pool, as this will require evolution on the part of local herbivores (Gilbert, 1977). Herbaceous crop plants, however, will not be a useful test of this hypothesis; they have had their defenses bred out of them to various degrees and thus should quickly accumulate their saturation herbivore load. I should also note that a newly introduced wild plant will not likely occur in a major monoculture, as is the case with crop plants. Therefore, requirements of herbivore coevolution with the host's physiological behavior, size, phenology, etc. may become much more important in slowing the rate of accumulation of the herbivore load than Strong et al. (1977) found to be the case with crop plants.

(16). On 11 August 1977 a healthy male tapir swallowed 95 intact seeds of *Enterolobium cyclocarpum* and 80 intact seeds of *Cassia grandis* (weight about 0.7 and 0.5 g each, respectively); for the following six days there was no trace of these extremely hard seeds in the tapir's feces except for two *E. cyclocarpum* seed coats. Hypothesis: the seeds were sufficiently slowed in their passage through the tapir's digestive tract such that they were sufficiently softened such that they were digested rather than dispersed. The various eddy currents (e.g., loops in the intestine) and pockets (e.g., caecum) could thus be highly adaptive in aiding digestion of seeds too hard to break with the teeth. Furthermore, large animals commonly thought to disperse hard legume seeds may well be extracting a high price in seed predation; there have never been studies of what percentage of the seeds ingested actually survive the voyage through the animal.

IN CLOSING

I cannot resist commenting on the classes of administrative effort that I feel we lack in tropical animal-plant studies. First, I feel that we have quite enough hypothetical biology on the books. We desperately need information on the pragmatics of what is actually happening out there. I can generate, with a little help from my friends, a computer model that will predict anything; for example, a model can predict that increased productivity should increase species richness and that increased productivity should decrease species richness, or it can predict that a predator should increase its specificity as prey gets scarce and that a predator should decrease its specificity as prey gets scarce. It all depends on what natural history facts you plug into the assumptions. Let's go out and get those facts, and ask what is their frequency distribution among real mem-

bers of real habitats and guilds. Of course, we should be gathering the facts in respect to questions, but let's not let the airy-fairy castles in the sky block out the sun.

Second, many kinds of tropical animal-plant studies involve systems with patterns or cycles that will not be apparent until tens of years of data on the same individuals in the same habitats by the same investigators have accumulated. Funding for more than three years, and often more than two, is largely nonexistent unless you pay for it out of your own pocket. NSF states that they cannot tie up funds for long periods. Well, if NSF will give me $40,000 in direct costs to spend this year, there is no reason why it should not give me $40,000 in direct costs to spend over the next ten years in $4,000 per year bits. They have paid out the money the first year and that is that. I would like to explicitly appeal for the establishment of grants of that structure, grants that will float with the investigator wherever or whenever transient. There are many long-term studies that I am now setting up for the last 30 years of my research life that could have had another 12 years on them had this sort of funding been available for this explicit purpose in 1965. Without this funding, we have the ironic situation that the shorter the time I have left to do research, the more likely my funding is to be sufficiently secure that I can set up such studies without having to worry about having the funds to census them annually.

Third, I would like to repeat a call (Janzen, 1977e) for some kind of internationalized and centralized chemical identification service, analogous to the great museums and their contained identification services. Secondary compounds and nutrient analyses of plants are to animal-plant interactions what Latin binomials are to ecology and evolutionary biology. A contemporary tradition is developing whereby natural products chemists are being prevailed upon with ever-increasing frequency to do secondary compound determinations by ecologists and evolutionary biologists. And in a manner exactly analogous to whole-organism taxonomists, the natural-products chemists are being swamped. With a very few exceptions, and these exceptions tend to have a very short half-life for obvious reasons, their work is slow, interrupted, variable in quality, and heterogeneous in coverage. Their primary commitment is not to those field biologists who send in a box of this or that at highly unpredictable intervals. Virtually all identifications are done gratis as a personal favor. When there is more than one class of secondary compound in the plant part, and this is normally the case, the specialist concerned can readily isolate and identify within only one class. It is as though I had sent a tanager gut off to a museum and the determinations came back reading 15 *Solenopsis geminata* subsp. *goofus*, 12 creepy-crawlies, 14 slimies, 1 blob, and 102 hardies. There is no Museum of Secondary Compounds nor is there any laboratory in the world that for a routine service charge will survey plant samples for kind and concentration of secondary compounds.

Yet if entomologists, ornithologists, primatologists, ecologists, etc. are to give secondary compounds the attention that they have long deserved in understanding animal-plant interactions, such an identification service is essential. I am certain that the highly inconclusive nature of the tens of thousands of pages of

data that have been gathered on feeding biology of herbivores is largely due to (1) the impossibility for humans to identify secondary compounds with their own senses, and (2) the difficulty of getting such compounds identified by other workers. I have seen much evidence that field workers would be quite willing to conduct the feeding experiments and observations to place secondary compounds in their proper perspective if they could get them identified easily.

If connected with the appropriate institution, I suspect that such a laboratory could be established for less than 1 million dollars, and I suspect that its running costs could be largely met through charges for determinations. A spin-off would be research on the new compounds encountered and the purification (at cost) of large amounts of certain compounds to then be used in field trials. Such a facility won't happen unless some small and dedicated body of people take it on (e.g., people centered around E. A. Bell, King's College, London; T. Mabry, University of Texas, Austin; P. Waterman, University of Strathclyde, Glasgow; R. Cates, University of New Mexico), and they won't take it on unless ecologists and evolutionary biologists can create a climate in the funding agencies for its support.

So in conclusion then, where are the promising new areas in tropical animal-plant biology?

(1). Take systems that are already very well known in terms of general natural history and taxonomy, and apply current concepts of ecology and population biology to them, rather than picking on one of the many largely unexplored "Oh My" systems.

(2). Figure out how tropical plants survive in pure stands, rather than worry about the mixed species stands.

(3). Use the organisms to tell you about the rates and kinds of harvestable productivity, and work backwards from this to expose the underlying causes; again, for the mercenary at heart there may be some powerful lessons here on how to competitively exclude our competitors or increase the yield from apparently low productivity sites (e.g., a rubber plantation may be such an example, discovered quite accidentally).

(4). Apply the multitude of hypotheses and ideas that are appearing in secondary compound chemistry to tropical plants and the animals that feed on them. Do not be too fascinated with the generalities; let's get some frequency distributions of results first. Furthermore, it won't happen unless we can get some sort of an International Museum of Secondary Compounds, Isolation and Identification.

(5). Stop thinking in terms of optimal seeds, fruits, flowers, reproduction times, seed crop sizes, etc. We have to start thinking in terms of optimal distributions in space and time for these parameters (as well as for other parts of plants and animals). Most plant parts are confronted by a set of animalian challenges or mutualists, not just one.

(6). At the risk of being labeled a Darwinist fanatic, I would emphasize the value of looking very hard for the adaptive significance of traits that we regularly take for granted (e.g., variation in seed size within a seed crop, rotting of fruits, duration of ripening times for fruits, seediness of fruits). It has been

my general experience that pessimism about the adaptive significance of a trait is strongly correlated with ignorance of the natural history of the organism.

(7). All the contemporarily fashionable ideas about parental investment, optimal parentage, sibling rivalry, etc. all apply to plants as well as to animals. In the tropics, animals play an enormous role in plant breeding systems and much of their obscure interaction with plants may become clearer when we come to understand what are the driving forces that determine which plant is to mate with which plant.

(8). We need much, much more natural history of tropical plants and how they interact with animals. I don't mean miscellaneous field notes of which beetle was found sitting on which plant, but rather natural history directed at interesting questions in ecology and evolutionary biology; we have plenty of them.

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ECOSYSTEM RESEARCH IN THE TROPICS

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Perhaps the biggest problem when discussing ecosystem research is, just what is ecosystem research, and how does it differ from other branches of biology? A traditional definition of ecology is that it is the study of interactions between organism and environment. Platt (1974) and Jordan (1975) have argued that this definition is inadequate, because a large portion of all biological and agricultural research and a significant fraction of medical and engineering studies can be construed to be studies of the interaction between organism and environment, whether or not the studies are really ecological. For example, a sewage engineer might convince a local town council that he is an ecologist because he studies interaction between bacterial concentrations and river flow, and therefore he could claim competence to prepare an environmental impact statement on the effect of sewage outfalls from new housing developments on the stream that passes through the town. We would argue that he is not competent because ecological problems resulting from sewage disposal are not limited to bacterial concentrations, but include such phenomena as eutrophication and resulting changes in fish populations, and recreational and economic use of the unpolluted river.

If "the study of interactions between organisms and environment" is an inadequate definition of ecology, because many diverse types of scientists study such interactions, what then is the unit of study that is unique or basic to ecology? One system of classifying units of biology is the hierarchical approach. In this system, for example, the basic unit of study for cytologists is the cell, and the basic unit of study for the morphologist is the organ. For ecologists, the basic but it must have definable limits inside of which there are integrated functions. ecosystems."

If our definition of ecology is "the study of ecosystems," we must then define ecosystems. An ecosystem is an integrated unit, consisting of interacting plants and animals whose survival depends upon the maintenance of biotic and abiotic structures and functions. The unit does not necessarily have to be isolated, but it must have definable limits inside of which there are integrated functions. What are these ecosystem functions?

There are three functions upon which ecosystem ecologists focus their attention: energy flow; nutrient cycling; and water flux. Nutrients, energy, and water also are studied by physiologists, but what sets ecosystem ecology apart is the structure that supports these functions. Physiologists study flows of energy, nutrients, and water in individual organisms, whereas ecologists study them on an ecosystem scale.

In using this definition of ecology we do not mean to say that the only truly ecological studies are those which follow energy, nutrients, and water through

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ecosystems. We certainly do not exclude those scientists who focus on species interactions and population dynamics. What is important is that the investigator maintains a holistic perspective.

Maintaining a holistic or ecosystem perspective, in the sense that the scientist considers all ecosystem aspects, is what sets an ecologist apart from scientists of other disciplines. For example, if we see a scientist studying the aquatic life in a river close to a sewage outfall, we could tell if he has the ecological perspective by asking him his objectives. If he answers that he is trying to protect human health by getting rid of harmful bacteria, he may be an environmental scientist, but he is not an ecologist because he is not considering all the ecological effects of the sewage entering the river. If he answers, in effect, that he is trying to protect human health by keeping man's life support systems functioning, in this case perhaps by preventing eutrophication and thereby maintaining a downstream fishing industry, he has the ecological perspective. He considers the implications of the problem, above and beyond the direct and obvious problem.

A Tropical Ecological Hypothesis

Because the title of this symposium is "Perspectives in Tropical Botany," we should relate tropical botany to ecosystem research in the tropics. Tropical plants are, of course, the base of the food chain in tropical ecosystems. Tropical plants also recycle nutrients from decomposing organic matter on the forest floor and make the nutrients available to the animals. It is in this sense that we tie tropical botany to tropical ecology.

We are going to talk mainly about our own ecosystem project in the tropics, but we will place it in perspective by comparing it with other tropical ecosystem research projects. The overall objective of our project is to study the structure and function of an Amazonian rain forest, so that increased ecological understanding of the ecosystem can contribute to more effective applied management in future years. However, we are not interested only in the applied aspects, we are interested in the basic nature of Amazonian ecosystems, what temperate-zone man expected to find there, what he actually found, and how the differences can be explained in terms of ecosystems theory.

Temperate-zone man has equated tall forests and large trees, and diverse flora and fauna with productive landscapes. When he encountered the Amazonian rain forest, he was impressed by the mass of vegetation and variety of organisms, both of which exceeded his temperate experience. He concluded that the tropics must be very productive. However, when he converted tropical forests to agricultural plantations, yield declined drastically. Why?

Temperate experience suggested that the yield was related to soil fertility. Therefore, the problem must be in tropical soils. And indeed, the amounts of essential nutrients could be very low. But then, how could luxurious tropical forests survive on such poor soils?

Ecologists have hypothesized that development and survival of lowland tropical rain forest is through nutrient-conserving mechanisms that maintain the essential elements within the biomass of undisturbed forests, and that the destruction of these mechanisms by cut-and-burn agriculture results in rapid

loss of nutrients, with a resultant loss in ecosystem productivity. While this concept is almost popular knowledge, the hypothesis has never been tested. The major emphasis of our Amazonian ecosystem research program is to test this hypothesis and to identify the nutrient conserving mechanisms which operate in the undisturbed tropical forest ecosystem.

The San Carlos Project

The field site of our project is near San Carlos de Río Negro, in Amazonas Territory of Venezuela. The site is within the north-central drainage basin of the Amazon River. There are two principal forest types in the area, both about equally important in terms of area. One is the tierra firma forest, located on laterite covered with a thin layer of sand or gravel. Species diversity is high, and biomass is close to 400 t/ha (Jordan & Uhl, in preparation). The other type is located on sand, with a podsol B horizon at about one meter depth. During heavy rains, the water table reaches the soil surface in this type. Biomass and species diversity is less than on the tierra firma site (Klinge, 1976).

The experimental approach is as follows: We have a series of experimental and control plots on both soil types. We have measured the nutrient inputs, outputs, storages, and transfers of the major ecosystem compartments in these plots for one year. After one year, the experimental plots were cut and burned following the traditional local practices. In the podsol site, some areas were planted to rubber plantation and others were abandoned for secondary succession studies. In the tierra firma site, the experimental area was planted with typical crops of the area, manioc, pineapple, plantain, and a few other species.

As a result of our observations and measurements during the first three years of the project, it has become apparent that a well-developed root mat and humus layer which occurs on top of the soil surface plays a key role in nutrient conservation and recycling. We hypothesize that:

(1.) The root mat and humus layer on the forest floor act as an exchange column to prevent leaching of nutrients until the nutrients can be taken up by the roots.

(2.) Mycorrhizal fungi play a role in the direct transfer of nutrients from decomposing litter to roots.

Other nutrient conserving mechanisms that we are examining are:

(3.) Algae and lichens living on the surfaces of leaves and bark play an important role in nitrogen fixation of the forest.

(4.) There are virtually no nitrifying bacteria in the forest. Maintenance of nitrogen in the ammonium form is a nitrogen conserving mechanism (Rice & Pancholy, 1972).

(5.) There is either a sulfur fixing capability in the forest such as sulfur fixing bacteria, or the forest is being depleted of sulfur, since loss of sulfur through stream flow far exceeds input through rainfall.

(6.) Sclerophylly and evergreenness in the tropical rain forest are nutrient conserving mechanisms.

(7.) Many nutrients move from leaves back into the stems before the leaves fall.

(8.) Trees are adapted to the oligotrophic environment in that roots are physiologically very efficient in extracting nutrients, utilize a low oxygen environment, and, at least in the podsol site, are resistant to flooding.

(9.) Insect predation of leaves is low in the podsol site, and only slightly higher in the laterite site. These low predation rates may be due to plant compounds such as alkaloids and polyphenols. These compounds may act as nutrient conserving devices in that it is more economical for the plant to manufacture secondary compounds than it is to manufacture a new leaf in the nutrient poor environment.

(10.) Termites play an important role in redistribution of nutrients in the forest.

(11.) In the tierra firma site, the rough root mat on the soil surface causes the newly fallen leaves to lie at various vertical angles, with the result that the leaves resemble somewhat the shingles on a pitched roof. Rainfall and throughfall quickly pass over these "shingles," minimizing the opportunity for leaching by water, and allowing more time for recycling by mechanisms such as mycorrhiza.

Other hypotheses are emerging relevant to the treated experimental areas:

(12.) Despite the fact that the roots of secondary successional species are primarily in the upper layer of mineral soil and not on the soil surface, they have an extremely high capacity for nutrient uptake. When the forest is cut, but allowed to immediately begin the successional process, the successional species can recover a large proportion of the nutrients released by the decaying organic matter. However, if the ecosystem is cropped, most of the nutrients will be lost, either through leaching or through harvesting.

(13.) Life spans of slash and burn farms are determined primarily by the decay rate of organic matter and root biomass in the soil which supplies nutrients to the crops.

In addition to development of these ideas, comparison of the data from the two forest types with different soil conditions has led to hypotheses regarding nutrient cycling in the podsol sites versus the lateritic sites, as well as hypotheses regarding cycling in these ecosystems compared to other forest ecosystems:

(14.) In the laterite sites, standing crop, productivity, and rates of nutrient cycles are slightly higher than in the podsol, seasonally flooded site, possibly due to lesser extremes of water conditions and anaerobiosis.

(15.) Highly sclerophyllous vegetation with highly inclined leaves located in patches on the podzolic soils, with a xerophytic aspect, reflect an extreme where there occurs drastic alternations between drought conditions and flooding with anaerobic conditions.

(16.) Consumption of vegetation by insects in the podsol site is lower than in the laterite site.

(17.) In both sites, rates of productivity and nutrient cycling are lower than on more fertile soils in both temperate and tropical regions.

(18.) Although biomass in both sites is relatively low in comparison with other forests, the forests are climax in the sense that net ecosystem productivity is zero.

(19.) The biomass of the forest is limited by the available pool of nutrients and the capability of nutrient-retaining mechanisms to prevent their loss.

Other relationships that have emerged as a result of our studies of water balance and biomass, which were necessary steps in the quantification of the nutrient budget, are:

(20.) Rate of transpiration in trees is independent of species and site, and depends only on sapwood area per unit of forest floor.

(21.) Biomass of all tree species can be described by a single regression on $(\text{diameter})^2$ (height) (density).

Organizational Aspects

The San Carlos project is a cooperative study between institutions in Venezuela, the United States and Germany. The project is headquartered at Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (I.V.I.C.), in Caracas, Venezuela. Other participating Venezuelan institutions are Universidad Central de Venezuela, and CODESUR, a branch of the Ministry of the Environment. The German participating institutions are the Max Planck Institute at Plön, and the World Institute of Forestry at Reinbeck (Hamburg). Participation of United States institutions is being coordinated through the Institute of Ecology, University of Georgia.

Funds for the project are coming from the Organization of American States (OAS), UNESCO, CONICIT (Venezuelan Science Foundation), United States National Science Foundation, Deutsche Forschungsgemeneinschaft, and indirectly through IVIC and CODESUR.

The project has been designated a MAB I pilot project by UNESCO because of the progress that has been made in relation to other MAB ecosystem studies in the tropics. It is also part of the Humid Tropics Forest Project of the OAS, which includes projects in Brazil, Trinidad, and Colombia.

The project was started in 1974, at just about the time the International Biological Program (IBP) Biome studies were drawing to a close. In designing the project, we strove to take advantage of the lessons learned during the operation of the IBP studies. The strengths and weaknesses of these programs have been discussed by Mitchell et al. (1976).

In order to build upon the wisdom gained from the IBP studies, we did the following:

(1.) First of all, we returned to the old-fashioned method of designing the project, to test hypotheses, rather than build the project around a technique, such as was done with systems analysis in the IBP studies.

(2.) Secondly, we confined our ecosystem model to a single process model, rather than model many processes and populations and attempt to integrate them into a single model, as had been done with little sucess in the IBP studies.

(3.) Thirdly, we kept the project small, in comparison with the United

States IBP studies. In many cases, the large scale of these studies had caused them to be unwieldy from the point of view of management.

Another organizational factor which weighs heavily in biological research in the tropics, and especially ecosystem research because of its magnitude, is the problem of scientific imperialism. For many decades, if not for centuries, North American, European, and Japanese scientists have visited Latin American, African, and Southeast Asian countries, collected data, specimens, and samples, brought them back to their home countries, and bestowed little or no scientific benefits upon the host countries. Over the years, this has resulted in a resentment in the tropical host countries because knowledge derived from such studies or whole efforts did not contribute to the improvement of personnel and infrastructure in the respective countries, and did not aid the development of similar projects run by their own people. Many times it has been due to lack of local scientific personnel, but often the projects did not have the policy of improvement of local capabilities (Budowski).

This problem was discussed during the 1973 Costa Rican meeting of tropical ecologists, during which ecosystem research in the tropics was evaluated and recommendations for future research was discussed. The proceedings of this conference were later published in the book *Fragile Ecosystems* (Farnworth & Golley, 1973).

As a result of the recommendations in this book, our ecosystem project was specifically designed to contribute to the scientific infrastructure of the host country. For example, instead of bringing samples back to the United States or Germany for analysis, we have set up our own analytical laboratory in Caracas, and trained a team of technicians to operate it. Part of the data processing is taking place in Caracas, but copies of all original data are kept in Caracas, so that it can be used by other investigators.

We have limited the number of North American and European visitors, with the intention to increase as much as possible the number of Latin American participants. Further, we make an effort to have counterparts for visiting scientists, so that the visitors experience will not be lost to Venezuela. For example, we have initiated a soil microbiology program, in which the visiting United States microbiologist is traning a Venezuelan investigator to follow through and complete a study of nitrifying bacteria in the Amazon forest.

Comparison with Other Ecosystem Studies

In general, most of the values of the ecosystem parameters which we have obtained so far are equal to or somewhat lower than values from other tropical ecosystem studies.

Total living biomass on the tierra firma sites near San Carlos averaged 391 t/ha. Other biomass studies of tropical rain forests have produced values within the same range or somewhat higher. In Puerto Rico, Jordan (1971) estimated the biomass of one site of a montane forest to be 228 t/ha, while Ovington & Olson (1970) estimated three in the vicinity to be 324, 209, and 269 t/ha. Dry weight of above ground biomass in two Panama forests were 377 and 276 t/ha (Golley et al., 1975). In Ghana, Greenland & Kowal (1960) estimated

biomass of a secondary forest to be 289 t/ha, while two evergreen tropical forests in the Ivory Coast, constituting part of the French project at the Banco and Yapo reserves, were estimated to have above ground biomasses of 465 and 425 t/ha (Huttell & Bernhard-Reversat, 1975). In the Pasoh forest of Malaya, above ground dry weight of biomass was 664 and 475 t/ha on two plots (Kato et al., 1974), considerably greater than our values for San Carlos. In evergreen seasonal forests of Cambodia, total biomass in two stands was 415 and 348 t/ha, (Hozumi et al., 1969), while in Thailand values ranged from 326 to 404 t/ha (Ogawa et al., 1965).

Near Manaus, Brazil, Klinge & Rodríguez (1973) found about 900 t/ha fresh weight including roots. If we assume the moisture percentage is the same as in San Carlos, then total dry weight would be 585 t/ha. Rodin & Bazilevich (1967) in their survey of global biomass put an average value for tropical forests greater than 500 t/ha. The world biomass summary by Art & Marks (1971) gives similar high values.

Leaf fall values which for the San Carlos forest are around 5 t/ha/yr are in the low part of the range of values for tropical forests. For example, in the Ivory Coast Forest Project, leaf fall rates were 8–10 t/ha/yr (Huttel, 1975) and in the Khao Chong forest, Thailand, rates were about 12 t/ha/yr (Kira et al., 1967). In the eastern Amazon Basin, near Belém, rates were 7.4–10.7 t/ha/yr, but in the central basin near Manaus, the rate was 6.7 t/ha/yr (Klinge, 1974), only slightly greater than the value for San Carlos. Jordan & Murphy (1977) have presented litter fall values from 27 tropical forests. Most values are greater than 7 t/ha/yr, and there are quite a few values greater than 10 t/ha/yr.

Rates of soil respiration at San Carlos are about 400–500 mg C/m^2/hr, within the range encountered in Thailand.

Concentrations of nutrients in water fluxes such as throughfall, stem flow, and soil water are generally less than were found in tropical forests in Puerto Rico (Jordan, 1968), Panama (Golley et al., 1975), and Ghana (Nye, 1961).

The most striking difference between our study, those of Klinge (1973), those of Went & Stark (1968)—all in the Amazon Basin—and those studies in other regions of the tropics is the apparent importance of the root mat and humus layer in the Amazon forests. As we mentioned previously, the root mat appears to play a key role in the recycling of nutrients. Yet in other studies outside the Amazon region, the presence of a surface mat, if present, is not noted or emphasized.

The evidence that we are obtaining, then, is verifying the idea that the Amazon forest is severely nutrient limited, and that low biomass, low litter fall, and low nutrient concentrations, all are adaptations to the oligotrophic condition. In addition, mechanisms such as the above-ground root mat and direct recycling by mycorrhiza are adaptations to help the ecosystem survive in the nutrient-poor conditions. The implication is that destruction of the Amazon forest on a large scale will cause an irretrievable loss of nutrients and consequently of the ecosystem, because large scale clearing destroys the nutrient conserving mechanisms.

Future Tropical Ecosystem Work

What about future ecosystem research in the tropics? It is typical for a presentation to conclude with a plea that it is especially important for the particular research discussed to receive more recognition and greater support. We will not break with this tradition.

In general, ecosystem research in the tropics is too fragmented, with the result that the studies do not have the political effectiveness that they should, in the sense that the results of ecosystem research should influence political planning for a region. When a group of scientists work together on a single ecosystem problem, such as they did on the Hubbard Brook study (Bormann et al., 1968), the final impact is much greater, even if the findings are very controversial as they were in the Hubbard Brook study (Aubertin & Patric, 1974). For this reason then, we make the plea for less fragmented research and more integrated efforts, with the ecosystem approach being a natural integrating device.

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PERSPECTIVES IN TROPICAL BOTANY: CONCLUDING REMARKS

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It would be unrewarding to attempt to summarize the rich sampling of perspectives in tropical botany that has been provided by the five papers in this symposium. Each should be read for what it has to offer in insight and in vistas for future research. In these concluding remarks, I wish instead to offer some thoughts on the general state of tropical research, and to attempt to put them into a global perspective.

Judged from statistics about relatively well known groups of animals and plants, there are likely to be about twice as many species of any group in the tropics as in temperate regions. About 1.5 million kinds of organisms have been given names during the first 225 years of our effort to do this, and there are probably at least twice as many that remain to be named. Of these, perhaps two-thirds of the estimated 1.5 million organisms of temperate regions have been named, but no more than one in five of those in the tropics.

In 1975, the following estimates of cumulative destruction of tropical forest were made by the Food and Agriculture Organization (FAO) of UNESCO (Sommer, 1976):

Original area of tropical rain forest (world): 16 million km^2
Area in 1975: 9.35 million km^2 (reduction of 41.5%)
Destruction to 1975:

Latin America	36.6%
Southeast Asia	38.1%
Africa	51.9%
India, Sri Lanka, Burma	63.3%

A doubling in population size is projected for all tropical countries by the end of the century. Although inroads are being made into the difficult problems of expanding food production in the tropics, the Environmental Fund predicts that annual population growth will outstrip growth in food production in each of the major tropical areas of the world through 1985, which is as far as they have attempted to project. Statistics such as these lead to forecasts such as that of the destruction of all moist tropical forest in the Philippines and Malesia within 5 to 10 years, and throughout Indonesia within 15 to 20 years. Worldwide, it appears likely that virtually all tropical forest will be destroyed or at least irreparably damaged by the close of the century, although it will probably still persist in a few local areas, perhaps including portions of the Amazon Basin, by that time.

Projected rates of growth in population, food, and energy lend little hope for a reversal of these trends. For example, the FAO estimates that by 1985 some

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26 countries, with an aggregate population of 365 million people, will be unable to produce enough food to prevent gradual starvation. In addition, if most tropical forest will have been removed by the end of the century, what of the quarter to half million people who make their living at present by slash-and-burn agriculture in this forest?

Tens of millions of people in the world starve to death each year at the present time, and with these trends being what they are, it appears likely that hundreds of millions will starve in tropical countries during the coming two decades. The countries involved, which will mostly become preoccupied with life-and-death questions of food and energy, will be unlikely to be able to divert many of their precious financial reserves to the study of the forests and other natural ecosystems, even though the sustained productivity of their lands ultimately depends upon such knowledge (cf. Janzen, 1973). It therefore will apparently be up to developed countries such as the United States to devote the necessary capital to gaining whatever ecological knowledge it might be possible to accumulate during these critical years. Only by doing so will it be possible to gain a measure of world stability for our successors in the twenty-first century.

In the light of these facts, it would appear that there is little or no chance for the long-term preservation of a significant sample of tropical diversity. Many of the two million or more species of animals and plants that occur in the tropics and which have never been catalogued or given a scientific name will become extinct before they are collected once; however, since our generation alone will be able to deal with them, we should make every effort to preserve samples for those who will follow us to study and to use to answer a host of questions about the diversity of life on earth that have not even been formulated yet.

In terms of formal inventories, the rates of completion of tropical floras are such that, when compared with the rate of destruction of the forest themselves, they appear pathetically low. We are simply not devoting sufficient resources to these projects to allow for their completion in a timely fashion. It would be highly desirable to step up our input into them, especially by involving more of the citizens and institutions of the tropical countries themselves in the project and by securing adequate funding from whatever sources appear possible. No matter how energetic these efforts may be, however, it is clear that the inventories will not be completed in time to provide a basis for further biological generalities or extrapolations of higher order: questions about biological interactions must be asked *now*, if we are to learn anything about the functioning of ecosystems upon which a growing proportion of the human race depends for survival.

Tropical biology of all kinds must receive a high priority in both research and training programs, at every level, and within every competent body. We can learn about the nameless and unknown plants and animals of the tropics only for a few more decades; our survival depends directly upon an understanding of the way in which they maintain a stable productivity in the hottest and rainiest areas of the world, often on extremely infertile soils. The attainment of such knowledge by our own generation is of crucial importance, since our children and grandchildren will not be able to help.

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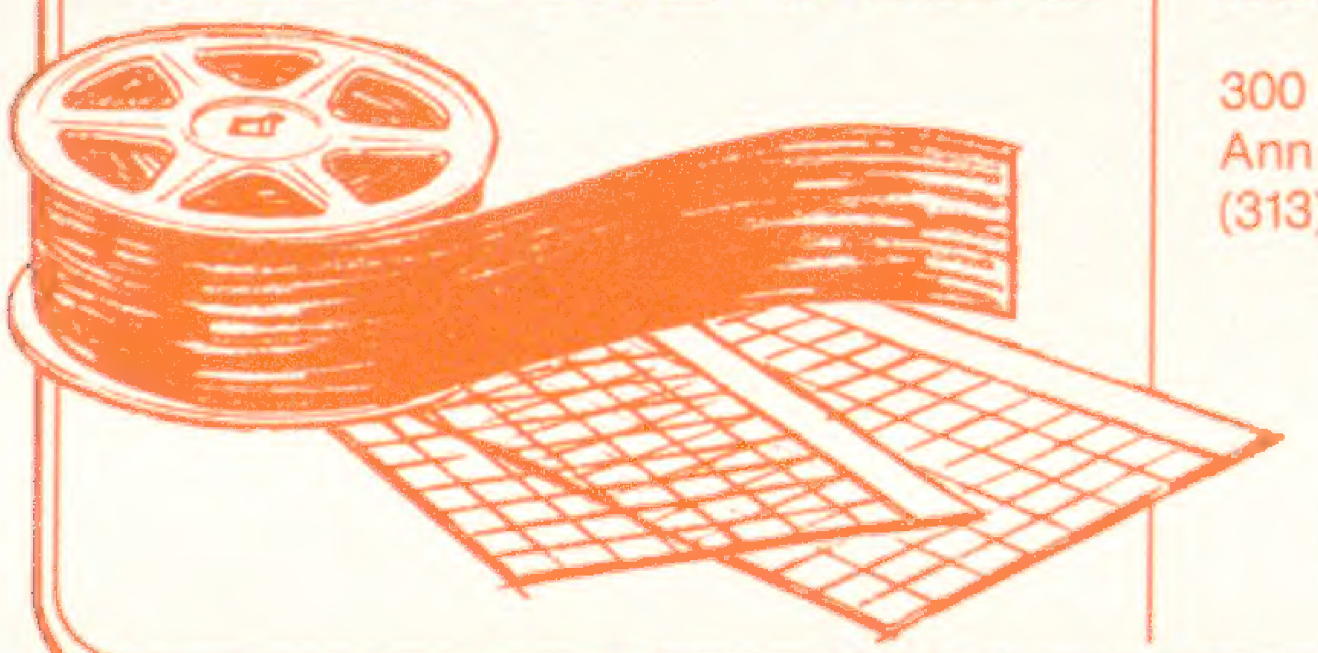

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